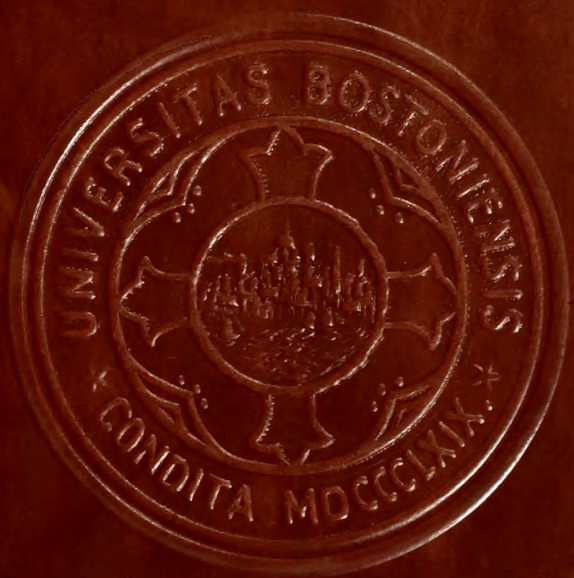

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Thesis

PARASITIC and SAPROPHYTIC SEED PLANTS

by
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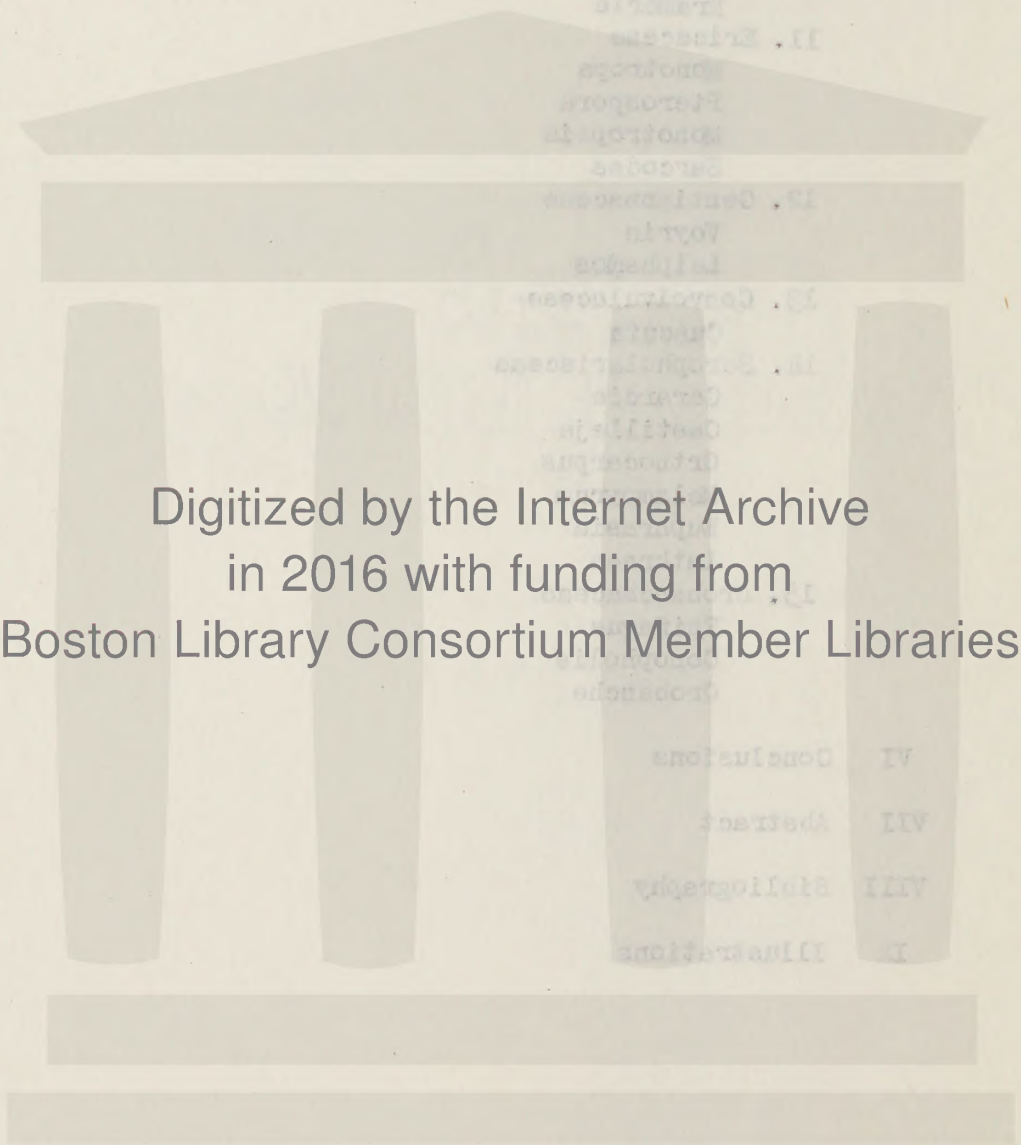

I INTRODUCTION

Someone has said "the world is one great bouquet," and yet many of the most interesting wild flowers go unnoticed or unrecognized. Among the dependent seed plants are species such as Orobanche or Cancer root, drab in color and neither abundant nor beautiful enough to attract the attention at first, and the minute Arceuthobium of New England which was passed by until 1871. Once noticed, however, their unusual appearance and characteristics arouse great interest.

The term "wild flowers" is quite inadequate to describe these plants which do not gain their nourishment in the customary way. Nevertheless, they are truly "wild " because of their unwillingness to be civilized. Their dependent habits make it impractical or impossible to cultivate them. Occasionally they are savage, like the common dodder, making their brazen way as outcasts of society. Others are modest flowers of delicate color and texture living on decaying leaf mold in the dark depths of the forest.

These eccentric flowers make up a freakish but delightful array. They have a great diversity of habitat and form. Dependent plants are not limited to one group, but appear scattered through the successive forms of the plant kingdom.

In spite of their many differences and unrelated origins, all the plants gaining nourishment from others have similarities and like features which link them together.

The purpose of this paper is to make a comparative study of the phanerogamic families which are not completely independent, to observe the

distinguishing characteristics of each, the similarities and analogies of all, and particularly to investigate their methods of gaining nourishment.

II Heterotrophism

Heterotrophism is the condition in which the organism is dependent on others for its nutrition.

Some plants obtain their foods from other living organisms and are parasites. The degree of parasitism varies greatly. Some are complete parasites, gaining all their nourishment from the host. The parasite gains the advantage while the host may be merely deprived of some of its own nourishment, or injured, or killed. The parasite has organs of some sort which act as roots or suckers to obtain nutriment from the host. These may be attached to various parts of the host. There are two main types, one parasitic on the roots of the host, and the other parasitic on the aerial parts of the host. The root-like structures may grow into the tissue of the foster plant or form attachments to its surface. In this way, the parasite is able to obtain sugar, mineral salts, and water. Organs adapted for gaining nourishment from the host are called haustoria.

Some plants are only partial parasites. They contain some chlorophyll and can thus make some of their own food. They rely on the host for some of their necessities. For example, having no roots in the ground, mistletoe lives on the branches of its host and must obtain water and mineral salts from the juices of the host. It contains chlorophyll so that it can carry on photosynthesis to manufacture its own foods.

Some plants, which are parasites on the roots of other plants, in addition to the suckers gaining nourishment from the host, have roots which act in the ordinary way, taking in materials from the soil. Some of these may live as holophytes ordinarily, but become parasitic under crowded conditions

or only when in the vicinity of the roots of a suitable host. These are facultative parasites in contrast to the obligate parasites which cannot exist other than as parasites.

Parasites often show a specific selection of hosts and are frequently confined to one particular species.

Symbiosis is the living together of two dissimilar organisms. In mutualism, this is advantageous to both. When one party receives much benefit and the other little or none, or is harmed, this is termed commensalism. A partnership harmful to one of the partners is called antagonistic symbiosis. In a broad sense, it includes parasitism, the extreme form in which the parasite gets all the advantage.

Some plants obtain their nourishment from decaying organic matter. These are saprophytes. They are lacking in chlorophyll and so cannot carry on photosynthesis to obtain their nourishment in the ordinary way. The color of the whole plant may vary from pure white to red, yellow, or brown, due to the presence of pigments ordinarily masked by the green chlorophyll. Saprophytes have a rhizome or underground branch in coral form or a mass of numerous entangled underground stems. They have no true root hairs and obtain nourishment by means of an intimate relationship with a fungus, the hyphae of which closely surround the roots and take the place of the root hairs. Elliot(22) says that such fungi are abundant in good, well-grown forests. The fungus threads extend in every direction, breaking up and decomposing the leaf mold. The relation between the fungus and seed plant is known as mycorrhiza. A definite species of fungus may have its strands entering the roots of the saprophyte and piercing the cells, or these may only penetrate short distances between the cells.

It is often difficult to determine whether a plant is independent, parasitic, or saprophytic. It is a problem to tell what the relationship between two plants is. The obvious parasite may be performing useful functions for the host, such as shading it from too hot sun and conserving moisture. Epiphytes, air plants which grow without connection with the soil on the trunks or limbs of other plants, may take the sunlight and moisture needed by the host or form a decay center by harboring fungi and insects.

Many plants depend on others for mechanical support depriving them of sunlight and moisture and adding an increased burden. By their abundance they may injure the host.

The parasitic plants discussed in this paper, however, will be confined to those groups which actually take materials from within another plant.

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III Parasitism in General in Seed Plants

Parasites and saprophytes appear scattered through the plant kingdom. In the Phanerogams, they are prevalent in several widely separated families. Macdougall and Cannon (54-p50) present the following figures. One genus in every two hundred includes parasites. About 2,500 species of parasitic seed plants are known, which is about two per cent of the recognized forms and a thorough investigation would probably double this number. A much wider category of plants is included in the mycorrhizal forms. These symbiotic arrangements between fungi and roots are accompanied by alterations in the shoot of the higher plant, much like those characteristic of parasites.

In the long succession of plant forms, parasitism has appeared and reappeared in various forms and habits. Many of these have been unsuccessful in evolution, but many have prospered.

Kern (47-p116) points out that the classification of plants physiologically as autophytes, parasites, or saprophytes does not coincide with a taxonomic one. Upon morphological grounds parasites are variously distributed in the taxonomic series with independent or saprophytic forms. If our classification can be regarded as representing phylogenetic relationships, their arrangements not only suggest the evolution of parasites from free-living ancestors but also indicate many separate points of origin.

The presence of free stages in the life-cycle of many parasites (among cryptogamic plants), the frequent occurrence of temporary parasitism, and close morphological resemblances between some independent and some dependent forms afford abundant evidence to justify such a point of view.

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from independent ancestors without any intervening saprophytic condition, such as probably existed in the evolution of the fungi. The first step may have been the absorption of water and food materials, the taking up of complex foods being a later development.

Freeman(26) describes the possible origin of Cuscuta. Remote ancestors of our common Morning Glory found that their stems, closely twining about another plant of an entirely different species made possible the transfer of stems fluids from the plant about which these stems are wound. This transfer was improved by suckers. Gradually, a complete food supply was possible and the now-confirmed parasite found leaves and even chlorophyll unnecessary, and thus we have the parasite family of dodder. Even today the individual dodder begins life as a seedling autophyte, but it perishes unless it finds a host.

Macdougall and Cannon (54-p2) give three ways in which mechanical adhesion could make parasitism possible. (1) Roots growing thickly interlaced in soil might unite or penetrate each other. (2) Adventitious roots arising from internodes at any place on the aerial stems might pierce the bodies of other plants. (3) Seeds lodging in the bark or in the wounds of a plant might germinate and send absorbing organs into the tissues of the possible host.

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of chlorophyll, although it still retains the flower and seed characteristics of its distant relatives. This partnership is known as a mycorrhiza.

In a similar way, the fungus probably attacked the root systems of other plants. Not all the invaded plants died, and some were able to resist the attack and even to gain so that the relationship came to have mutual benefit. Now there are various species of plants representing all stages in this development, varying from saprophytes to independent plants.

There are many factors operating to make parasitism possible. A succulent plant would be more subject to attack than those lacking in reserve material in solution. The most recent studies on this by Kusana (50) show that parasites, particularly the Rhinanthaceae and Santalaceae, carry a large water-balance in specialized tracheids.

An unequal osmotic concentration may operate in determining parasitism. Harris and Lawrence (36) studied the osmotic pressure of the tissue fluids of three genera of Loranthaceae and their hosts. The osmotic pressure was calculated from the depression of the freezing point of saps extracted by pressure from previously frozen tissues. In the great majority of cases, the freezing point lowering of the parasite is distinctly greater than that of the host. In other words, their tissue fluids are characterized by higher osmotic pressure. The osmotic pressure of the tissue fluids of the leafless species is distinctly lower than that of the juices extracted from the leaf-bearing forms. While higher osmotic pressure of the sap of the parasite is a general condition, it is not necessary for at least the temporary success of the parasite. The parasite should be able to draw from the relatively dilute solutions in the stem in competition with organs of actually higher osmotic pressure, except at periods

when the supply of soil moisture is limited.

Harris (34) found that Cuscuta may have tissue fluids with lower osmotic concentration than its host. A possible explanation is that Cuscuta may have the property of developing only when soil moisture is adequate to supply the needs of both host and parasite. The desert forms of both Cuscuta and Loranthaceae have a higher osmotic concentration of leaf tissue fluids than those of moist regions.

Although Phoradendron is widely distributed in the arid south west, it is all but absent on the creosote bush, Covillea tridentata. Harris, Harrison, and Pascoe (34) thought that this might be due to the osmotic concentration. Their tests showed that the sap of Covillea has a higher osmotic concentration that that of the usual hosts of the species.

There are three relationships to be considered concerning the osmotic concentration, which are that of the parasite, that of the host, and that of the physical properties and water content of the soil. There is a low correlation between the tissue fluids of the parasite and those of the host. This may be due to an actual adjustment of the tissue fluid properties of the parasite to those of the host or to some extent merely due to the influence of environmental conditions.

For parasitism to become established, the members of the pair would have to come in contact. Originally they must have had a similar habitat and growing season.

The relative acidity and electrical conductivities of the host and parasite have been considered as possible factors in the formation of a union. Harris, Pascoe, and Jones (37) found that the specific electrical conductivity and chloride content were higher in mistletoe than in the host.

In Cuscuta, Harris (34) found that these were lower than those of the tissue fluids of the host. Macdougall and Cannon (54) found that in producing parasitism artificially, the relative acidity of the two plants appeared to be of little or no importance in the determination of their capacity to form a nutritive couple.

The ability of the parasite to form a means of gaining nourishment from the host would be a necessity in parasitism. This would include the penetrative power of roots or shoots and the ability to form haustoria. The resistance of the host would be important in the determination of parasitism. Soft tissue or tissue with much intercellular space would be more easily penetrated, while tough bark and the formation of wound tissue would be inhibitors to the parasite.

Another factor in determining parasitism might be the ability of the seeds to germinate. Cannon (6) found that germination of Phoradendron seeds might occur on leaves, thorns, old bark of dried stems, or on branches of the mistletoe itself. It therefore appears that the nature of the substratum does not influence the germination of this parasite. Seeds chancing to lodge on another plant, and which were still able to germinate, might become parasitic.

There are three possibilities for the genetic basis of parasitism. It might be the result of a gradual change over a long period of time. It could have been an inherent weakness towards the loss of chlorophyll and the loss of the ability to make starch for itself, or towards the loss of the ability of the roots to grow deep enough to get sufficient water. It may be the result of a sudden mutation which could require the plant to become parasitic. Different parasites may have originated in different

ways, and one species may have had many factors in its origin. In the passage of time new pairs of plants, which could become parasites, would be brought into association. Experiments in artificially producing parasitism have shown that the tendancy toward parasitism is strong.

Some of the alterations which have produced parasitism may have been decidely unfavorable and these plants would die out if the alteration were irreversible. Kern (47-p17) states that there is no evidence in plants of a parasite ever conquering the habit and returning to the usual existence.

The many changes which accompany the development of parasitism are more or less common to all the parasitic and saprophytic seed plants. Kern (47) points out that parasitism is strongly linked with degeneration. Parasites are more or less degenerate according to the extent of their parasitism. In the seed plants there is evidence of somatic degeneration, consisting chiefly of reductions or atrophies of the shoot and root, even in the forms which are only partially parasitic, while those which are fixed parasites may be still further reduced, the root failing to develop, the shoot remaining unbranched, the leaves lacking chlorophyll and frequently appearing as colorless bracts. This is accompanied by a decrease in size and number of stomata.

Individuals parasitically nourished are usually smaller than independent individuals of the same or closely related genera. Boeshore (3) traces the gradations in the condensation of the stem and root systems, and amount of foliage. In the more independent species of Gerardia, the stem is one to four feet tall, well formed, typically dicotytedonous, and the leaves are large and ovate-lanceolate. In Gerardia aphylla, a very marked condensation occurs. The stem is slender, rather wiry, unbranched, and

from six to eighteen inches in length. The leaves are much reduced in size, are scale-like, and closely applied to the stem. Condensation is more marked in Harveya and Hyobanche in which the stem is only four to six inches in height. Both are parasitic, have scale-like leaves, which may even be reduced to functionless scales. In Lathraea the vegetative axis has become a rhizome two to six inches long with hollow scale leaves. In Orobanche the vegetative axis is an enlarged tuber one and one half inches or less in length and covered with densely crowded scales. In Aphyllon the vegetative axis is reduced in thickness to scarcely more than one-fourth inch or less, and about one inch in length. The number of scale leaves is reduced to about five or ten.

Another change in parasitism occurs in the cell structure of the conductive tissues, which become adapted for securing fluids from the host. The phloem becomes more abundant than the xylem.

Boeshore (3-p145) points out that in parasitic and saprophytic families, there is often a transition from a several-celled central type of placentation to a one-celled parietal type.

Some seeds lose the power to germinate except when in contact with a suitable host, and the seedlings cannot continue growth without a source of nutrition. Some parasites have developed to the point at which they cannot continue existence unless in contact with a host of a certain species. The selectivity seems to be more or less correlated with the degree of parasitism. Species of Gerardia which are more or less root parasitic have a wide range of hosts, including Grasses, Composites ect. Orobanche minor parasitizes forty four species. Conopholis americana of the same family always parasitizes roots of Quercus borealis, and Percival (68) believes

that its seeds will germinate only in the presence of the host root tips.

The parasitic habits of many of the seed plants cause injury to their hosts, and thus create a problem by harming other plants which human beings consider more valuable. Species of Cuscuta and Orobanche cause serious injury to crop plants such as alfalfa, clover, lespedeza and tomato. Root parasites on trees, such as Conopholis and Epiphagus, seem to do little or no damage to the host probably because they are so small in proportion to the size of the tree. Many of the Loranthaceae cause injury to their hosts. The dwarf mistletoes have made serious inroads on the conifers of the Northwest. Much ofthe injury is due to malformations such as galls, cankers, and witches' brooms. One trouble parasites cause is to open the way for insects and fungi which may do great harm.

Many people in considering parasitism in seed plants give the term a general social significance and condemn all parasitic plants as lazy outcasts, unwilling to make their own food. One writer (87) speaks of parasites as "the worst and most insidious of all plant criminals, the vampires who fatten themselves upon other plants, and secure their nourishment by sucking the life-blood of their victims. Like feminine vampires of fiction, they are often very beautiful."

The wholesale condemning of parasites is unfair. A parasite rarely kills its host as this is committing suicide. It cannot live without the host, so is not benefited by harming the host. The host usually sets up a defense mechanism.

Many of the parasites have certain praiseworthy features from man's point of view. Some of them, lacking chlorophyll, can live on the floor of the deep forest where no light reaches and ordinary green plants could not exist.

Cobb (47-p130) suggests that parasites could be used as an aid in discovering specific and generic relationships in physiology. The same or related species on different hosts may indicate a possible relationship or descent from a common ancestor of the two host plants.

Parasites and saprophytes might be considered to justify their existence by the beauty and interesting forms which they contribute. The vivid crimson of the snow plant, among the earliest to shoot up through the dark soil, adds a bright touch of color to the drab scene left by winter. The twining dodder stem, always coiling from left to right, has aroused interest from early times, as is shown by the following quotation from an herbal (74-p21), "Doder is a strange herbe, without leaves, & without rootes, lyke vnto a threed, much snarled and wrapped togither, confusely winding it selfe about hedges and bushes and other herbes."

IV Artificially Produced Parasitism

Experiments producing parasitism artificially have been performed to study the relationships between host and parasite and to learn more about the possible origins of parasitism.

Peirce (67) experimented to find how an independent plant behaves when compelled to be partly or wholly parasitic. He grew Piscum sativum on a plant of Vicia Faba. The seeds of the pea were allowed to germinate until the radicles were one or two centimeters long. These were inserted in holes cut in the stem ofthe horsebean and sealed with plaster of Paris. Wet sawdust was put over this in dry weather. Control plants were grown in dirt. The bean-peas were much smaller and had only two or three peas in a pod. These were soaked in water twenty-four hours, and placed in wet sphagnum to root. They were then put on horsebean and grew into small but healthy plants. He found no tissue union between the host and parasite. The roots grew downward through the internodes and nodes, but did not reach the level of the soil. The roots branched less than in normal soils but provided sufficient water. No xerophytic characters were evident on the peas like those of the aerial plants of mistletoe.

Macdougall and Cannon (54) also induced parasitism experimentally with several desert plants. They found in grafting Cissus on Opuntia that the water-balance in these and other succulents of the region was greatest from December to March and from July to August. It was found advisable to set up unions during these periods, the greatest number of survivals resulting from the experiments started in February. They grafted Opuntia on Echinocactus, as the osmotic pressure of the sap of the former is higher than that of the latter under similar conditions. The facts obtained show

that it is possible to establish regenerated cuttings of a number of species in a dependent nutritive relation with the bodies of enforced host-plants. In some cases, the xeno-parasite formed roots which penetrated the tissue of the host. In other instances, absorption took place through the epidermal tissues of the submerged bases of the inserted slips. The development displayed by xeno-parasites was, in all instances, less than that of similar shoots autophytically nourished.

Macdougal (55) inserted regenerated cuttings of vines and cacti in cavities prepared for them in the bodies of other plants sealing them with plaster of Paris. When one form was induced to become parasitic on another, the host in every case had a lower osmotic pressure than that of the xeno-parasite. Regenerated cutting of a grape (Cissus laciniata) which undergoes secondary thickening in the stem to store food and water were successfully made parasites on Opuntia, Echinocactus, and sometimes on Carnegiea. Usually there was little evidence of forcible penetration of the tissues of the host. In all cases, the layer of tissue, one or more cells in thickness, nearest the roots was found to be dead and more or less disintegrated.

Macdougal (55) also found several cases of chance parasitism among the desert plants. In one case, the seed of an Opuntia Blakeana apparently germinated in the axil of a branch of Carnegiea gigantea, the giant sahuaro, where it took root. Some of the roots reached a distance of one foot, partly enclosing the base of the branch. One went directly into the tissue of the sahuaro to a depth of over six inches, being completely submerged and cut off from air. There was a dense network of secondary roots, none of which were in direct contact with living tissue. The contact thus made

with the sahuaro was undoubtedly the source from which the chief supply of solutions was obtained.

An Opuntia discata grew from the trunk of Acacia, probably sending its roots into a cavity formed by the decay of wood. (55)

Orchidaceae

This family is famous for its beautiful and strange members, and its unusual colors and curious shapes. Among the orchids are many parasitic and saprophytic species. These may have originated parallel with the epiphytic forms from a common ancestor, or the transition from a free-living epiphyte to a more dependent form could have been easily accomplished. The mycorrhiza associated with the roots or rhizomes of orchids are endotropic. The saprophytes are usually small plants with a simple yellow or reddish scale-bearing stem.

The orchids are herbs with parallel-veined leaves or scaly bracts clasping the stem. The flowers are irregular and have a bract at the base of the flower stem. The sepals and petals form two whorls and are often the same color so are difficult to distinguish. One of the petals differs in form and color, being an irregular, enlarged lip, which may be fringed, pouched, or bristled, often spurred, and is generally the most beautifully marked. Gray (30) explains its position by saying "The lip is really the posterior petal, but by a twist of the pedicel or ovary of half a turn, it is more commonly directed downward and becomes apparently anterior." The pollen is borne in one or more masses called pollinia.

The genus Corallorrhiza, commonly called Coral-root, portrays its dependency by its lack of green color. Ames (1) has revised this group. It is saprophytic in the rich humus of forests sometimes changing its habit to become parasitic on roots. These may also be saprophytic, using only material of other plants already in a state of decomposition. No roots are present, but instead a much branched fleshy or brittle underground stem,

coral-like in appearance. From this arises a simple scape furnished with sheaths and flowers in a raceme. Baldwin (2) describes the four pollen masses as "soft-waxy or powdery, having no stalks or connecting tissue."

This genus is spread through the north temperate zone. Many species are common in New England and one species is found in Scotland where it is very rare.

The genus Hexalectris is somewhat similar to Corallorhiza. It has no chlorophyll and has a coral-like rootstock. It is saprophytic.

Hexalectris aphylla (Nutt.) Raf. (H. spicata) (Brunetta)

This is described by Gray (30), and Morris and Eames (59). The stout scape is brown, one to two feet high, with brown, short, truncate, sheathing scales. The large, handsome flowers are borne in a fairly wide, loose raceme. The sepals are yellow with seven purple, grayish-brown striae on the face. The upper sepal is longer and narrower. The petals are delicate yellow with seven fine purplish-brown striae, and are obovate to oblanceolate. The lip is yellowish-white with four thin lines of violet on the wings and three pairs of purple ridges each side of the median line interrupted by white, and is three-lobed. Its flowering season is from July to August. It is found in rocky open woods, especially limestone areas from Virginia and Kentucky southward.

Cephalanthera (Phantom Orchid)

This is briefly discussed by Hylander (42-p612). It is a stout, white plant with a creeping rootstock and fleshy roots. The leaves are reduced to long sheathing bracts. The plant is terminated by a spike of yellowish-white flowers, each with the lip and other floral parts typical

of the orchid blossom. It is found around the Mediterranean, and in California.

Neottia (Bird's Nest Orchid)

This is a saprophyte mentioned by Elliot (21) which has a mass of entangled underground stems resembling a bird's nest.

Several other dependent forms among the tropical orchids are discussed by Ames (1). Aphyllorchis benguetensis is apparently parasitic on pine roots in pine forests. Aphyllorchis pallida is a slender leafless plant similar to Corallorrhiza maculata. The bracts are tubular, loosely sheathing the stem. There are twelve to twenty flowers in loose racemes, grayish with purple dashes. It is found in Java, Perak, Pahang, and Singapore.

Didymoplexis pallens is a slender saprophyte with large tubers often serially arranged. The whitish-brown stem is leafless bearing several filamehtous roots at the base, and scattered reddish bracts. The flowers are white or flesh colored in loose racemes. The sepals and petals are adherent forming a tubular perianth . In fruit, the ovary becomes greatly elongated, possibly for the purpose of carrying the ripening fruit above the decaying vegetable matter in which the plant grows. Collections were usually made in the vicinity of bamboo, and it seems to be a saprophyte or partially so. It is often found growing on rotten bamboo in bamboo hedges near brooks. It is a native of Formosa, Java, Perak, and from Calcutta to Sikkim.

Cystorchis aphylla is also a saprophyte. The stem is salmon colored to white, clothed with sheathing acute bracts. The tips of the perianth are white and the petals and upper sepals lightly adherent. It is saprophytic on earth about decaying logs in forests. (1). It is found in Java and Malacca.

Galeola altissima, a saprophyte of the Malay peninsula, has long thin stems which climb to the tree tops where they fix themselves by air roots springing from the nodes. A richly branched panicle ends the shoot.

Burmanniaceae

Burmanniaceae is a highly differentiated family with a remarkably wide tropical distribution. It contains small, thin-stemmed annual or perennial herbs which, except for some species of Burmannia with narrow green leaves, are leafless saprophytes. These saprophytes have a red, yellow, or whitish stem bearing scales. Mycorrhiza are associated with the roots. A few species are root parasites.

Burmannia occurs in the tropics of both the old and new worlds, and passes beyond the tropics in North America. It contains some species that are leafless saprophytes growing in the humus of old forests. The saprophytic genus Gymnosiphon occurs in the tropics of all three great continents, and the allied genus Dictyostegia is found in America and Africa, while other genera are confined to Asia, Africa, or America. Several of these are monotypic. The greatest development of the family occurs in Malaya and Brazil. (75-p344)

Thismia Aseroe is a Malayan saprophyte. It has a system of branching, leafless absorbing organs extending over a substratum of decaying leaves, to which they are attached. These send up pink, scaley axes bearing a single or several flowers which are orange-yellow. The mycorrhiza of the absorbing organs are endotrophic. The outer cortical cells are almost filled with a coiled mycelium of swollen, irregular, moniliform, mycorrhizal hyphae. From these, slender hyphae, often spirally twisted, extend inward and suddenly swell out into conspicuous intercalary bladder-like bodies. Inside this are conspicuous dead mycelial masses. These fungi are living organisms within the host, and receive nutriment from the external substratum.

Santalaceae

The Sandalwood family is chiefly tropical and has strong tendencies toward parasitism. Many are root-parasitic, attaching themselves to the roots of trees, shrubs and grains for their sustenance. Self-parasitism is common among the santalaceous forms. Some are parasitic on the branches of trees.

The genus Comandra (Bastard toad Flax) is composed of low, herbaceous perennials, most of which are parasitic or partially so. The greenish-white flowers are bell or urn-shaped. Moss (60) describes the Comandra livida Richards and the Comandra Richardsiana Fernald as semi-parasitic. Pinus murrayana roots are parasitized by C. livida. The haustorium, by which attachment is made, thrusts aside the periderm of the host and pushes through the cortex and phloem to the xylem. A well-defined gland often appears in the haustorium and probably functions in the production of digesting enzymes. Comandra umbellata (L.) Nutt parasitizes the roots of trees and shrubs.

Nestronia umbellula Raf. is mentioned by Gray (30) as a low shrub parasitic on the roots of trees and occuring from Virginia to South Carolina and Alabama.

Thesium contains about 250 species, chiefly in the temperate zones, with its highest development in South Africa. The plants have usually narrow, one-nerved leaves.

Thesium humifusum (Bastard Toad-flax) is abundant in the British Isles. The seedling becomes attached to the root or rhizome of the host plant by suckers formed on the branches of the primary root. It often attacks cereals and other grains. (75)

Chabrolin (8) studied the germination of Thesium. He found that saprophytic fungi were necessary to soften the selerenchymatous part of the seed coat so that it could be broken by the swelling of the seed.

Buckleya is a genus of slender, fairly tall shrubs included in Small. (82) It has two-ranked branches and leaves. The leaves are opposite or nearly so, and the blades narrow, membranous, or entire. The dioecious flowers are small and greenish; the staminate in terminal umbels; the pistillate solitary, terminating branchlets. B. distichophylla (Nutt) Torr. is the species found in America. It is about two to four meters tall and is parasitic on the roots of hemlock. At one time Paint Rock, Tennessee, was thought to be the only station for this shrub, but this colony has been since destroyed and others have been found. It has been reported occasionally in sandy soils under hemlocks along the banks of streams tributary to the Holston and French Broad rivers in Virginia, North Carolina, and Tennessee. (44) Fernald (23) points out that the local species is distinct from the Japanese and Chinese species.

Loranthaceae

This is a family famous for its parasitism. There are three genera which are better known than those of the tropics. Viscum album is the mistletoe of the old world and Phoradendron flavescens that of the new. Arceuthobium is the dwarf mistletoe occurring on conifers.

The European mistletoe seems to have been known from earliest times. It may have been its strange habits of growth, its characterless yellow-brown color which becomes a beautiful gold color when sunlight shines through it, or its rarity, which aroused the curiosity of the ancients and led to many legends and superstitions about it. Monsch (58) tells of some of the traditions about mistletoe. There was one story in England that it was the wood from which the cross of Christ was made, so that it was cursed and condemned to live as the most despicable of plants.

Pliny wrote that it was held sacred by the Druids. They thought that it "kept away witches and evil spirits, and brought safety, good fortune and happiness if it did not touch the ground. Held in the hand, it invoked the appearance of ghosts and gave the possessor the ability to see and speak with them. It was put over doorways in homes as protection for the home and those passing through. It was thought to insure success in hunting.

The Romans decorated their homes with mistletoe in Saturnalia so the woodland spirits could come in from the cold. Peasants of Holstein and other places call it "Marentaken" meaning "branch of phantoms." There is a Scandinavian myth that the arrow which slew Balder, son of Oden and Frigga, was fashioned of mistletoe. The Gods were so angered by his death that they decreed the mistletoe to be a mere parasite. The berries were supposed to

be the tears of the lovely Frigga. Balder was miraculously restored to life and Frigga decreed that the mistletoe was guiltless and should be the emblem of Love so that anyone under it may receive a kiss. Muller (62) asserts "Youthful folk never forgot that mistletoe is an excuse for uninvited (?) kissing."

Fogg (24) says that mistletoe was used in the middle ages to fatten cattle. Muller (62) says it was thought to have great potency as a general panacea for all ills, including its power to cure barrenness in women and also in cattle. Decoctions taken internally or applied externally were believed to be effective, variously, in cures of itch, epilepsy, convulsions, general debility, weakness of visions, cramp, wounds, sores, antidote for poison, ad infinitum.

That their beliefs in the medicinal value of mistletoe may have some basis of truth, is shown by the fact that it contains a substance similar to digitalis. Rojo (76) found that extracts elevate the blood pressure and increase the coaguability of the blood. There is first a slowing of the pulse rate. The active principle is "quipsine." In experiments Viscum extract was injected into and around implanted tumors in mice, and destroyed the tumors in a high percentage of attempts.

The name mistletoe may be derived from the Anglo-Saxon "misteltan" meaning "a different twig" or "a bird-lime twig." The mistletoes have gelatinous viscid berries so that they will adhere to the bark of the proposed new host. These are spread largely by birds. The mistletoes often have a marked effect on their hosts, causing them to produce galls, witches' brooms, or woody rosettes. Mistletoe is the state flower of Oklahoma.

Viscum

Viscum album L.(European Mistletoe)

This is an evergreen parasitic shrub growning high on the branches of various deciduous and evergreen trees. It has yellowish-green leaves and inconspicuous flowers, which are succeeded by large glutinous waxy-white berries.

The morphology is described by Schönland (79). It is dioecious, the plants of the two sexes having on the whole the same structures. The axis of the seedling produces two cotyledons and a pair of foliage-leaves alternating with these. It then ceases to grow any further, but in the axils of the foliage-leaves, buds are produced which develop into branches the next year. Each branch bears at its base two, minute, opposite scale-leaves, the prophylls of the new shoot. Near the top of a branch two foliage-leaves are usually found, and they last normally only one season.

In about the fourth or fifth year of the life of a plant, a small capitate inflorescence is produced at the tip of each shoot between the two foliage-leaves, and normally consists of two lateral flowers at right angles to these leaves and a terminal flower. In the female flowers, the perianth consists of two dimerous alternate whorls of scale-leaves, which cohere, more or less, at the base. The two carpels continue the regular alternation. The male flowers are on the same general plan, but every trace of an ovary is absent. Each perianth leaf bears six to twenty pollen-sacs.

Pohl (72) presented observations and experiments on the method of pollination and nectar secretion in V. album. Evident nectar secretion, mostly during the night was observed in pistillate flowers. The discus-like

ring just below the stigma functions as a nectary, the liquid exuding through the few stomata. The nectar is very viscid. In the staminate flowers, no secretion of drops of liquid was observed. The flowers have all the characteristics of entomophilous plants; flag-apparatus, nectar, odor, sticky pollen, and insect-visitation.

Pollination occurs in the fall, but fertilization does not take place till the following spring. In August or September, the transparent, whitish berry appears. This is very attractive to the birds, probably because they last after other food sources are beginning to be depleted. Monsch (58) says that one thrush of Europe is called the "mistle-thrush" because of its feeding habits. The seeds are plentiful in mid-winter. The pulp is digested but the tiny seed has a strong coat and passes through the digestive tract. The semi-fluid dropping helps to imbed the seeds. The mucilaginous quality of the seeds makes them adhere to the bill and feet of the bird. The bird usually wipes them off on a clean branch. It hardens and anchors the seed to the tree.

Heim de Balsac (39) states that birds are the sole agents in the dissemination of V. album, although in France only three species feed on the berries. The fleshy fruit does not need the pulp removed in order to germinate, but requires the pulp for becoming attached to the branch and for the protection of the embryo.

Dalmon (14) points out that in a geologically homogeneous locality in Seine-et-Marne, frequented throughout by Turdus viscivorus, there is a sector in which Viscum album abounds and a sector where it is absent. There are evidently unknown, non-avian factors in the germination of the seeds.

The embryo in the seed begins growing through the soft part next to the bark and into the host. The root-like haustoria dissolve and digest their way, penetrating the host, and through the food conducting belt to the sapwood to reach the crude sap. The parasite must have water and soil constituents and may take some already manufactured food from the host. It is more vigorous in the second year. It is succulent when young, becoming brittle and woody with age.

V. album is widely distributed through Europe and Asia and is common in southern England. It is not found in Scotland, Ireland, and northern England, and Monsch (58) states that the explanation seems to be that these localities are not frequented by the winter migratory birds. V. album has many hosts among the deciduous trees, preferring apple and its relatives, such as hawthorne, crab-apple, service berry, and pear. It causes damage to the orchards in Herfordshire, northern France and Tyrol. In the Himalayas, it infests apricot and grape. Hanssen (33) states that it is rare in Norway, occurring at numerous points on the west side and one on the east side of Oslofjord, all near the shore. It attacks especially Acer planatoides, Pyrus malus, Sorbus aucuparia, Betula verrucosa, and certain species of Populus. All the stations are within the geological formation called the Oslofield. Heim de Balsac (39) says that the injury of V. Album to forest trees is negligible, but to fruit trees it is undeniable. For the protection of the latter, the regular cutting off of the parasite is recommended.

Other species of Viscum are present in the tropics. Zarorski (98) describes the autoparasitism of Viscum cruciatum Sieb. in the Moroccan Atlas Mts. Steenis (83) found Viscum articulatum infesting Fluegaa virosa in Sumatra. It also parasitizes other Loranthaceae, Evodia and Calotropis gigantea.

Phoradendron

Phoradendron flavescens (Pursh) Nutt. (American Mistletoe)

This is the leafy species of mistletoe found in America, corresponding with the European species but differing from it. It has its floral parts in threes, the sepals and ovary are adherent, and the clusters of flowers in spikes. It is dioecious with small flowers. Its branches sometimes grow rather large, forming bushy masses in the host trees. They are yellowish-green and bear thick, glabrous, obovate leaves of the same color. The leaves are persistent, so that the mistletoe shows up readily when the leaves of the host have fallen.

York (97) describes the germination of the seed. The seeds occur singly in the white berries which are borne on short axillary spikes. The embryo is distinctly dicotyledonous and is almost entirely embedded in the endosperm. It is abundantly supplied with chlorophyll. The cells in the radicle portion are rich in starch, while in the part surrounded by the endosperm, there is very little starch present. The walls of the testa are thick while the adjacent cells of the cotyledons are thin-walled. These cells which stain yellow with iodine, contain a fine granular substance and numerous plastids which are well supplied with chlorophyll. Thus the embryo is well supplied with food material for its immediate use on germination. Owing to the nature of its habitat, a period of time must elapse between germination and the establishment of the young plant on its host, when the ready food supply in the endosperm is likely to become exhausted. The purpose of the chlorophyll in the endosperm is evidently for photosynthetic work in order that the young plant may be supplied with food until it

becomes fixed upon its host. The cotyledons may remain embedded in the endosperm for a year or more and throughout the first year's growth of the plant, the peripheral cells of the endosperm are well supplied with chlorophyll. Thus besides a storage of food in the endosperm, there is a mechanism whereby more food may be provided for the young plant after the stored up supply becomes exhausted.

Monsch(58) describes the mature plant. The leaves are about two inches long, obovate, thick, leathery, very firm, and arranged oppositely in pairs. The tiny, insignificant flowers are dioecious and grow in short, crowded, grape-like clusters, often as early as February or May. In the globular three-lobed calyx are borne the sessile two-celled anthers as numerous as its lobes in the staminate flowers. In the fertile flower, the calyx adheres to the single ovary, which is one-celled and one-seeded. The male plant, with staminate flowers, is necessary for cross-pollinating and fertilizing the female. After this function, they dry up and disappear. The fertile flowers are followed by tight clusters of berries that ripen in September or October, and hang on for months. The berry is pearl-white, translucent, about currant size, and filled with mucilaginous pulp which hardens on exposure.

P. flavescens may harm trees, doing economic damage particularly to to nut trees and fruit orchards. Phillips (69) reports of its frequent attack on Emory oak in southern Arizona. It evidently gains entrance in the younger portions of the twigs. The clusters of mistletoe rob the infected limbs of a portion of their nutrition, often causing the outer portion to dwindle and die. Severe attacks stunt the trees, and may in extreme cases kill them.

Phoradendron flavescens is found exclusively in America. Gray (30) gives as its range, New Jersey and eastern Pennsylvania to Florida and New Mexico, inland in the Mississippin basin to Missouri, southern Indiana, and central Ohio. It infests broad-leaved trees particularly, such as oaks, maple, honey locust, tupelo, sycamore, elm, mesquite, hackberry, and cottonwood.

Williamson (96) told of the damage to cottonwood in the south by P. flavescens. Injuries are especially pronounced in the Red River Valley region of Texas and Oklahoma. Although the apparent injury is confined to the branches, the vitality of the whole tree is weakened through loss of nourishment withdrawn by the parasite.

Phoradendron villosum Nutt.

Cannon (6) gives a complete description of this plant. The leaves are borne in alternate pairs on stout stems, and consequently in reacting to the light, the leaves assume a more or less vertical position and become bent in petiole and blade. They are relatively thick of a yellowish-green color and are markedly brittle. The tips of the youngest leaves are projected beyond the growing point of the stem and their dorsal surfaces are closely pressed together. The surfaces thus in contact are inaccessible to light and are colorless, while exposed surfaces take on the color characteristic of the plant. The stomata which are found on both sides of the leaf, are of the xerophytic type and although they are considerably sunken below the surface, they are less so than those of the stem. In comparing the stomates of the mistletoe with those of the oak in regard to size and number, it is found that those of the former are about twice as large as

only approximately half as many to a given area as those of the latter. The number of stomates per square millimeter on each surface of the mistletoe leaf is about forty, while on the oak, where they occur on one side only, there are about eighty. The conductive system of the mistletoe leaf is poorly developed. The external color of the plant is entirely due to the coloration of the cuticle, and the chlorophyll is quite normal. The leaf of the mistletoe is mechanically very weak. This is partly due to poor development of supporting tissue, but chiefly to the prominent intercellular spaces. The stem is also weak mechanically, and is rather brittle so that it is easily broken. (6)

The mistletoe is attached to its host by haustoria, which in structure and in function show evident differentiation. The young haustoria ramify in all directions in the cortex of the host and they may even encircle the central cylinder. From these, others turn sharply toward the center of the host branch, and become partly enclosed by it. These are the so-called sinkers of the parasite and take the position of the host's medullary rays. The youngest cortical haustoria are composed throughout of thin-walled parenchyma. At the growing parts, the cells are elongated and secrete a solvent that is capable of digesting the host. These develop into sinkers and the haustoria seek only those cells which contain food; they are chemotatic. The position and number of sinkers are, to a great degree, and perhaps wholly, controlled by the permeability of the inner ring of fibers to the haustoria. The host cells in front of the tip of the sinker, in the cambium or bast, present a curved appearance as if under pressure. It is not likely that the sinker absorbs the adjacent tissue of the host to any extent, because no evidence of this was seen, and

further, there is an absence of epithelial cells, or cells having that general character in the sinker. The cells of the cortex remain alive and they probably die only as the parts of the host adjacent to them die. The walls of all of the sinker cells which are within the host are lignified. The thin-walled conductive system does not unite with the phloem of the host, sieve tubes do not unite with sieve tubes as in complete parasitism. There is however, a transfer of foods from the phloem of the host to the sinker by osmosis only.

Cannon (6) also points out that this mistletoe is a typical xerophyte. In the relation with the host, the advantage is apparently entirely with the parasite. At the season of the year when the oak leaves have fallen, and when the plant no longer makes food, the mistletoe might be called upon to give up a portion of the food which it was manufacturing, to the support of the host. He observed, however, that this was not the case. Material collected at such a time was examined, and found uniformly that those parts of the parasites which are the resevoirs of food contained the usual amount and that the oak tissues did not show in any way that food passed to the stem. There would be little chance for transfer, as the parts of the mistletoe containing food are in contact with either lifeless or dormant cells.

The degree of parasitism varies with the age of the plant and the part. The main part of the parasite lives on the water and mineral salts in solution, which it gets from the conductive system of the host, and the carbon from the air. A small portion of the cortical haustoria depends entirely on the host for its food. The seedling is a total parasite. If Phoradendron lost the ability to assimilate carbon and remained longer in germinating, it might become a complete parasite. The effect on the host

is to cause the death of the parts beyond. The destruction of the host tissues is brought about by living sinkers which absorb so much water, the more distal portions of the host are starved.

Phoradendron villosum occurs in California on several kinds of evergreens and deciduous trees, such as oaks, ash and cottonwood.

Cannon (6) believes that the distribution of the seed in P. villosum and also in P. californicum from tree to tree is probably always effected by the agency of birds, but its distribution in a tree may be brought about in another manner also. In cases where infection has occurred in the higher branches of the host, it frequently happens that numerous younger plants of the parasite will be placed directly under this pioneer, as if they were derived from its seeds. P. californicum is a desert species with the leaves reduced to scales. It hangs from the host in long pendant tufts and has straw-colored berries tinged with red. Its hosts include Acacia Greggia, Prosopis juliflora, Parkinsonia microphylla and possibly Covillea tridentata.

There are in all eleven species of Phoradendron in North America. P. bolleanum and P. juniperanum are desert species of the southwest found on various species of Juniperus, and Meinecke (57) reported that P. bolleanum nests high up in Abies concolor, often killing the leader and also the volunteers which spring up. P. macrophyllum has broad golden color leaves, and P. densum has small narrow leaves. P. rubrum has red or occasionally yellow berries. P. emarginatum has a berry with a warty surface, the plant of P. tomentosum is velvety-tomentose. P. chrysocarpum is a tropical species with white or yellow berries.

Parish (64) raises the question of why some species are leafy and others not. The fact that P. flavescens is leafy and P. juniperum leafless,

has been plausibly explained from the fact the first species growing on deciduous trees needs leaves of its own during the resting period of the host, while the juniper mistletoe needs none since it grows on evergreens. This is a satisfactory explanation, but it evidently needs amendment to make clear why P. bolleanum, growing on juniper should be leafy, while P californicum which is parasitic on the mesquite and other deciduous hosts is leafless.

Arceuthobium

This genus of mistletoe includes some of the most important parasites economically. It is called the Dwarf Mistletoe because of its diminutive size. Its leaves are reduced to scales and were it not for the great brooms it causes the host to form, it would be observed even less often. In the West where it attacks whole stands of conifers, foresters were forced to recognize it and study it.

The genus was first called Razoumofskya, in honor of a Russian botanical patron, but another genus already had been named for him with a similar name; so, to avoid confusion, the name was changed to Arceuthobium by Marschall von Bieberstein. This genus is restricted to the Northern Hemisphere and is found in greatest abundance and with the most variation in the West. There is only one species in the East.

Gill (27) describes the characters of the genus. The shoot arises from buds in the endophytic system after the latter has become well established. A single shoot may be simple or branched, and usually bears flowers until its second season. Primary side branches develop from axillary buds usually arising in pairs at those nodes which have previously borne flowers. The epidermis of the shoot is a single layer with stomata having their longitudinal axes at right angles to the longitudinal axis of the stem. The stem later has a cuticular epithelium without lenticels or stomata. The leaves are decussately arranged and reduced to opposite pairs of scales at the top of each segment. They are provided with stomata and completely covered with a heavily cutinized epidermis. The flowers may bloom either in spring or in late summer. The staminate perianth is usually three parted, and it is

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normally a lighter or brighter shade than the stems. The bright yellow pollen is borne on sessile anthers, which are on the ventral side of each perianth segment. The pistillate flowers are sessile, and normally axillary, usually single when terminal and in pairs below. The perianth is consistently two-parted. The ovary is inferior and unilocular. The blue to olive green fruit is usually ovoid and matures in the autumn.

Dowding (17) observed that the seeds of Arceuthobium americanum are shot out at maturity and may travel eleven yards. At less than two yards, they do not adhere, but do from two to eleven. Thus those travelling long distances have a better chance to adhere than those hitting the same tree on which they were borne. The force is caused by the giving way of a ring of tissue near the base of the berry.

The viscid mass of the seed provides for its adhesion and being hygroscopic may supply part of the water needed for germination. The seeds are jellylike after rainy periods, but gradually dessicated and shrivelled during dry weather. Peirce (67) noticed that the seeds would germinate on almost any substrata, such as dead branches or impenetrable bark, so it does not appear to be dependent upon stimuli from the proposed host, but more on proper moisture and temperature conditions.

Gill (27) found that the haustorium penetrates the host branch radially as far as the cambium and in its course sends out branches which ramify through the cortex irregularly. The sinkers are the parts in the xylem of the host and usually follow its medullary rays. The young parts are filaments of a single chain of elongated parenchymatous cells placed end to end. Later the xylem elements, vessels and tracheids, are differentiated towards the center. Thoday and Johnson (85) found no suggestion of a cambium or true phloem.

Arceuthobium pusillum Peck Peck (A. minutum, R. pusilla)
(New England Dwarf Mistletoe)

This is the famous miniature mistletoe of New England which was discovered so recently that new stations are still important. Dr. Gray (29) wrote, "It is curious that it should, after all this overlooking, be found during the same season by two persons, in three different counties, and so abundant as to disfigure or even to destroy the trees it infests." The observant discoverers of this plant were Mrs. L. A. Millington and Mr. C. A. Peck, who found it in different sphagnum bogs on black spruce. It is the only member of the Loranthaceae in New England.

After its discovery, many were on the lookout for it, but it was still considered rare in 1899. Shortly after that, however, many new localities and hosts were reported. In "Rhodora," 1900, were several articles on A. pusillum, reporting it on Picea mariana on the Maine coast, in Aroostook County, and Boylston, Massachusetts, and in Vermont on tamarack. In 1902, it was reported from Prince Edward Island (10), and Nova Scotia (64). In 1903, Eames (18) observed it in Connecticut growing on black spruce and tamarack. The color of the plants on the tamarack was brighter than that of those on the spruce, which were more slender. In 1904, it was reported from Rhode Island bogs (11). It is now known to be widely distributed throughout the New England states, and occurring south to Pennsylvania, north to Newfoundland, and west to Michigan.

von Schrenk found A. pusillum on Monhegan Island and on the nearby Maine coast where it occurred only within an eighth of a mile of the shore. He attributed this distribution to the fact that moisture was necessary for the proper discharge of the seeds. He describes the plant briefly. (80)

It is usually found on the younger branches of the spruces. Many stems grow out of the host branch sometimes twelve to sixteen in an inch. The stems vary in size and color, depending much on the vigor of the host branch. On the very strong branches the stems are dark brown, almost black, and vary from half an inch to an inch in height or more. On weaker branches the plants are paler in color, and usually have a more spindling shape. Other factors enter also, such as exposure to the direct rays of the sun, and the number of stems in a given length of host stem.

The mistletoe spreads by means of the endophytic system to the new growth of the host. Jack explains the age of the host and parasite. (43) In the autumn, small dark buds may be seen protruding through the bark of that portion of the twig which grew the preceding year. These develop into full sized plants the following year, having well-developed flower buds which open the succeeding spring; so that the living plants of the parasite are to be seen in three growing seasons before they finally drop off. In the autumn the fruiting mistletoe is found on the fourth year of growth back from the tip, while the plants for the next year occupy the next later growth or that of the third year preceding.

A. pusillum blooms in the early spring and the fruits mature in the autumn. This is a much shorter period than in some mistletoes in which the fruit do not form for over a year. Here, the blossoms are in mid-April and the fruit toward the end of September, when the seeds are forcibly shot out to re-infect the host or infect new hosts. The seeds are really shot out from the base of the capsule because the fruit changes its position to hang with the true summit downward when ripe. It is probably disseminated over a great distance by birds, as are the other mistletoes.

Eaton has noticed the peculiar distribution of A. pusillum in New England, (19) The thirteen southern New England stations form a narrow straight belt, closely paralleling and about seventy-five miles north of the terminal moraine of the last glaciation, and coinciding with a moraine indicating a major halt in the recession of the ice sheet. To the north, there is a wide gap of eighty to one hundred miles from which we have no herbarium material except from a single station, and there the range corresponds with another moraine. The distribution is determined primarily by that of its two principal hosts, Picea mariana and P. canadensis. There are striking differences, however, between the two ranges. Some secondary set of influences must operate to restrict the occurrence of A. pusillum to a range strikingly localized in comparison with that of Picea. The southern limit of the range of black spruce is roughly parallel with that of the mistletoe but thirty miles to the south. Eaton suggests that the occurrence of A. pusillum might be associated with or dependent on some fungus or bacteria requiring two hosts. If P. mariana were more susceptible to attack, this would explain the commoner occurrence of the mistletoe on that tree. The other host might be some bog associate, such as certain heaths, which have a strikingly similar range. These may be only coincidences or may be due to the scarcity of material. Other factors may enter, such as the habits of the seed spreading birds.

The principal host of A. pusillum is Picea mariana, but it is also found on P. canadensis, P. rubra, and occasionally on Larix laricinia.

It usually attacks the poorer or younger trees. In a bog at Concord, Massachusetts, a single young black spruce was infected, bearing both staminate and pistillate flowers. The reason for this exceptional occurrence,

how it got there, and why it did not spread to other trees, is still a mystery. It is strange that Thoreau did not discover this mistletoe, as he wrote in his journal of 1858, "About the ledum pond-hole, there is an abundance of that abnormal growth of spruce, instead of a regular, free, and open growth, you have a multitude of slender branches....with dense, fine, wiry, branchlets and fine needles....altogether forming a broomlike mass." (Eaton & Dow 20).

Many other species are found in the western part of America. Arceuthobium americanum Nuttall is often found on Pinus Banksiana and P. contorta. Its buds always arise terminally in small pedicel-like segments. Eaton (19) says of it, "it is slow to develop new infections on healthy trees, preferring trees fifteen years old or more."

A. oxycedri grows on Pinus and Juniperus species. Johnson (45) pointed out that the interval of fourteen months between the formation of the female flower and its dehiscence as a ripe fruit may be related to the fact that its hosts have a year intervening between pollination and fertilization. He observed the xylem connection between the host and parasite.

Because of the pathological effects of Arceuthobium species, forest and government workers have studied it a great deal. Weir (91) gives the following hosts and parasites as the most important.

A. laricis Piper on Laris occidentalis (Western Larch)

A. campylopodum (Engelm). Piper on Pinus ponderosa (Western Yellow Pine)

A. americanum Nuttall on Pinus contorta (Lodgpole pine)

A. douglasii Engelm. on Pseudotsuga taxifolia (Douglas fir)

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Arceuthobium often has a marked effect on the physiology of its host. Burls and brooms may be formed, and the tree is often stunted and sickly. Weir (92) believes that the harm is caused by the localization of food materials at the seat of infection, and the gradual reduction of the leaf surface of the host. Ten mistletoe brooms and ten uninfected branches were cut from a Western larch and thrown in a damp, shady ravine. The next June, nearly all of the foliar spurs ofthe brooms developed needles. A few on the uninfected branches barely protruded from the bud scales, and usually no leaves at all were present.

The result of a heavy infection of the trunk and branches is the death of the upper portion of the crown, causing staghead, or in some cases, the entire tree may succumb. It kills seedlings as the swellings cause the wood and bast tissues to become filled with pitch so that food materials cannot pass between the crown and roots. Great burls may be formed on the trunk. Infection of the branches causes a fusiform swelling, the first stage in the formation of a witch's broom. The mistletoe plant may die out on very old brooms, but the stimulus to abnormal branching may continue(91).

Burls formed in early life on the trunk cause suppression by reducing the food-transporting tissues, and often form open wounds. The extra weight of the brooms together with the accumulated debris, causes the branches to break off readily in wind and deprives the tree of its normal food supply(92).

Mistletoe reduces the seed production of the host and lowers the quality of the seed. Pearson (66) found that mistletoe infected blackjack showed a germination 17% below that of unaffected blackjack. Weir's germination tests(91) showed 65% for the uninfected,and 40% for the infected.

The burls and cankers often open the way for fungus or insect attack. Of 600 burls on larches, 278 were inhabited by serious wood destroying fungi. (91)

The only natural control of Arceuthobium is a parasitic fungus, Wallrothiella arceuthobii Peck, which probably tends to check the spread of this pest. It attacks the fruit at the apex and destroys it. (90)

The mistletoe thrives best in trees of uneven stands. In dense, close, even-aged stands, as in deep valleys, it causes less damage. It spreads more rapidly in the crowns of younger trees, owing to the greater number of twigs in close proximity susceptible of infection. (92) To reduce the chances of infecting young growth, all overtopping infected trees should be killed. Care should be taken that infected trees are not planted in regions where mistletoe does not occur. (93) Pure stands of a species subject to attack should not be established. The topography and prevailing winds should be considered in selecting a site for seed plants and nursery beds. (91)

There are instances of great regional infection which are sometimes sharply defined. Environmental factors may cause this.

Other members of this parasitic family are scattered all over the world. Loranthaceae are particularly abundant in the tropics where growth is luxuriant and hosts are abundant. Weir (94) found many Loranthaceae on Hevea Brasiliensis, the Para rubber tree, in the Amazon valley where they are very common. Seven species are found on Hevea: Dendrophthora poeppigii, Phoradendron crassifolium, Oryctanthus botrostachys, Phthirusa adenostemon, P. pyrifolia, P. amazonensis, and P. brasiliensis. D. poeppigii is constantly confined to Hevea and does much damage to it. It has pinkish-red

berries and greenish-yellow leafless stems. It is comparable to Arceuthobium.

In contrast to most tropical loranths, which send out roots from the gnarled point of attachment along the outside of the branch, giving off at short intervals, stout, sucker-like roots which penetrate the cortex, the Hevea mistletoe sends its roots directly into the cortex at the point of germination. This is characteristic of all species of the temperate zone and results in the formation of burls and cankers and the death of the branch beyond the point of infection.

The seeds have a mucilaginous coat to make them adhere. The primary root develops a sucker-like disc which is pressed firmly on the substratum. From the center of this sucker, a root or sinker appears which penetrates the cortex. This has meristematic tissue in the region of the cambium of the host. By intermediary growth, the root is able to elongate at the same rate as the increase of the branch in thickness. As the apex of the root is buried deeper each year by the increased increment of the host, the root appears to have actually forced its way into the wood. (94)

Injury to Hevea is a gradual reduction of the leaf surface,which causes reduction in height and diameter. New infections arise by germinating seeds, or by the extension of the submerged root system. Deep infection may cause staghead or the death of the tree. Infection of the main stem at an early age produces abnormalities, such as burls and contorted trunks.

Phthirusa brasiliensis is a leafy species on Hevea. These are controlled on plantations by removing infected branches, eliminating from associate crops and surrounding forest trees. It dies with the host, so it is not necessary to burn the cut branches. (94)

Seeds of some mistletoes found on Hevea contain as high as 20 per cent of their dry weight of almost pure rubber.

Other species are found on horticultural plants. Cacao is attacked by Phthirusa pyrifolia and Oryctanthus ruficaulis, orange and limes by both of the above and P. brasiliensis. The mango is frequently attacked by P. pyrifolia. Struthanthus flexicaulis, a vining species, if of common occurrence on both the wild and planted cashew. Oryctanthus botyrostachys is of considerable importance on avocado.

The parasitic genus Korthalsella, a member of the Loranthaceae, is found in New Zealand. (84) The three species are small, tufted, parasitic plants, two to four inches high, leafless and glabrous, with jointed stems. The flowers are minute, borne in groups of one male and four female together, two groups forming a whorl at a node. Seed distribution is ineffective, and the plants are therefore of localized occurrence. Germination frequently takes place when the seed is shed onto the parent plant, resulting in a sort of cannibalism. The New Zealand species have passed the minimum of reduction and are on the road to extinction.

Rafflesiaceae

This family has developed parasitism to the highest degree. Rafflesia was first discovered by Sir Stamford Raffles in 1818, on the Manna river in Sumatra, where it is known as the "Devil's Siri box"! This flower is not only unusual because of its extreme parasitism but is a strong competitor for the title of the largest flower of the world. The blossoms are quite spectacular, often three feet or more in diameter. The petals are fleshy, reddish colored, immense, subrotund structures, being twelve inches from base to apex, and having about one foot from the insertion of one petal to the next. It has no leaves, consisting entirely of the single huge flower in the shape of a shallow bowl and the endophytic system.

It possesses an unpleasant odor similar to that of tainted beef. This attracts flies which hover about it and apparently lay eggs in it. The nectary is large; Cooke (12) estimated that it would hold about twelve pints.

The seeds of Rafflesia find lodging against a horizontal root which lies close to the surface of the ground, or in a crevice of the trunk or branches.

The seed germinates, sending a primary root into the bark, which branches in the cambium of the host, and forms a circular band of tissue which completely surrounds the ring of vascular bundles. Externally, all that is visible is a ring-like swelling under the bark.(42) These branches have no need of conducting tissues, the cells being individually nourished, like those of the cambium, from adjacent tissues. They are, therefore, composed only of chains of thin-walled parenchymatous cells. Branches penetrating wood find starch in parenchymatous cells, and can survive; those in bast have no such stores and soon become inactive and dead. These branches

give rise to the buds which pierce the bark and develop into flowers eventually. In these buds and flowers, are conducting tissues of two sorts, tracheids and sieve tubes, which are directly united with the corresponding tissues of the host. (48) Dean (16) compares the vegetative body which is completely with the host to that of a fungus mycelium. Rafflesia is parasitic on the roots of figs and other trees in tropical Asia, several species being found in Sumatra, Java, and Borneo. (53) R. Manillana is found on the Phillipine Islands.

Picki-Sermolli (70) has described the parasitism of R. tuan-mudae on Cissus. One flower was thirteen centimeters in diameter on a Cissus which was thirteen millimeters. The imbedded part of the parasite is a broad cone, its apex penetrating the host plant to the pith. The cortex of the host is destroyed in the region of contact. Later vessels and sieve tubes bend around the cone. Rows of elongated parenchyma cells from the Rafflesia push into the cambium, xylem, and phloem of the host.

Cartellieri (7) has studied the absorptive system of R. Brugmansia of Java and Borneo. It consists largely of filaments of single rows of cells. The infected tissue of the host is in the form of a hollow cylinder. The parasite is especially well-developed in the wood at the border. The parasite spreads by threads of a single row of cells, that go forward first in the cambium. It grows in the cambium, wood, and very actively in the phloem of the host. Sometimes papillose curved tips, like haustoria, appear.

Pilostyles is a smaller form with many species, some of which are parasitic on Mimosae.

Pilostyles aethiopica is parasitic on twigs of the caesalpinus Berlinia paniculata. Strands without definite form run through the host tissue

sending out small branches, which grow radially against the wood and gradually become enclosed by this as sinkers. There are no foliage shoots, as all buds bear flowers. P. Haussknechtii has a more reduced vegetative body. It lives as a parasite on species of Astralgus. The flower shoots appear on the basal portions of the leaves. In the younger stages of development, the flower buds sit upon a cushion-like irregular mass of tissue, called the flower cushion, which is in direct union with the tissue of the host leaf. After flowering, these cushions die away. The intramatrical body of the parasite consists of simple cell-strands, chiefly in the pith of the host, but also forcing branches into the vascular bundles, penetrating the medullary rays and spreading in irregularly tangled filaments ending in the young flower-cushions. (28-p225)

Cytinus is another genus of this family. Two species are found in Mexico. Other species are found in South Africa and Madagascar. (53)

Hydnoraceae

This family contains only two genera. Both of these are root-parasites. It is sometimes included in the Rafflesiaceae, from which it is distinguished by the structure of the androecium and of the ovary, and by the presence of perisperm in the seed.

The genus Hydnora has eight species. It is found in Africa and the Malagasy Islands. Prosopanche has a single species found on the pampas of Argentina. The vegetative structure of both genera consists of a branched creeping rhizome growing from the point of attachment to the woody root, generally that of an Acacia or Euphorbia. From the rhizome spring large, fleshy, solitary flowers which project above the surface of the ground. The flowers are bisexual, with a whorl of three or four thick, fleshy, perianth-leaves united below into a tube which springs from the top of the ovary. (75)

Balanophoraceae

This is a family of root-parasites in the tropical woods or savannahs. The plants are leafless and without chlorophyll. The vegetative organs are reduced to fleshy, yellowish or reddish branched rhizomes. The rhizome is attached by suckers to the woody root of a host plant. Occasionally, the rhizome bears scale-leaves. The inflorescence is borne on an erect cylindrical axis projecting above the ground. It usually originates in the interior of the rhizome and after breaking through remains surrounded at the base by a sheathing outgrowth. When young, it bears numerous scale-leaves. The small flowers are generally crowded in a head or spike and they are sessile or have short stalks. They are unisexual, and may be monoecious or dioecious. The male flowers usually have a simple perianth of three or four leaves united below into a tube. The female flowers are generally naked. (75-p71)

Little is known about the method of pollination. Some species are visited by insects. They are probably attracted by the smell; Sarcophyte sanguinea of South and East Africa resembles the odor of decaying fish. Other species are wind-pollinated. (75-p73)

There are fourteen genera in the Balanophoraceae. Balanophora is the largest genus. It is found in the Indo-Malayan region and extends into tropical Australia and the Pacific Islands.

Balanophora nipponica, a native of Japan, is parasitic on the roots of Acer morifolium. The young galls have radial cell strands, extending out to the cortex of the host. Neighboring strands come together there to form a cushion which is the rudiment of the protuberance. At first, there is only one cushion per gall, but later there are five or ten. These

cushions rupture the cortex and expand. Their cells are wholly meristematic at first and later differentiate to vascular strands. (88)

Cynomoriaceae

Cynomorium is found on the shores of the Mediterranean, and on the Central Asiatic steppes, growing on the roots of shrubby or herbaceous salt-loving plants. The plant is a brilliant color. (75-p74)

Lauraceae

Cassytha is the only parasitic genus in this family of otherwise autophytic plants. Cassytha is an herb much like Cuscuta but apparently not related to it, except that they may have had similar circumstances leading to their origins. Rendle (75) describes it as having slender, cylindrical stems, attached by suckers to their host plant; leaves are absent or scale-like. The small flowers are generally collected in heads or spicate, having three sepals and three petals. As usual in this family, the petals are much larger than the sepals. The perianth tube is little developed in the flower but increases considerably in the fruit, forming a succulent outer covering.

Cassytha paniculata is a leafless parasite on the needles of Pinus radiata in New Zealand.(56) Although it appears not to harm well established trees, it can kill newly planted ones. It may be eradicated by burning off the land before planting.

Connaraceae

Cannon (54) studied Krameria, a desert plant of the Southwest, and found it to be parasitic. It was previously thought to be autotrophic. It is one of the most common desert shrubs. It usually occurs near another species, but not so close as to attract attention. It is less than one meter high, and bears small leaves. It produces flowers in the summer and fruits abundantly. It is well known for its commercial value, being used for many things, suchaas the adulteration of wine and tanning. It has no recognized habitat preference, although found mainly on slopes where its favorite host, Covillea tridentata is most abundant.

The roots of Krameria are shallow and attack only roots of hosts near the surface.

The roots branch little, are smooth and are dark red due to the presence of pigment in the cells of the cork. They are mechanically weak. Sometimes the roots coincide closely with the roots of another plant. In places, they are flattened and form cushions of tissue in contact with the host, and haustoria arise from these. The distal ends of the haustoria usually comprise a group of two or more sinkers. The cells at the distal end of the sinkers serve as links which unite the adjacent vessels of the host to the ducts of the parasite and thus the apparatus of water-conduction from the host to the parasite is completed. The ducts of the host turn into the tip of the sinker for a short distance, and groups of cells of the haustorium encircle and terminate the ducts.

The seedling is independent for an undetermined period. It does not form root-hairs. Haustoria do not appear on seedlings which are growing

independently of other species but if possible hosts are associated with the young plants, haustoria formed freely, and apparently without contact with the host. Various protective reactions appear in the host after the attachment has been formed, although the decadence of haustoria is frequently to be traced to an insufficient supply of water. (54)

Ericaceae

The heath family includes primitive shrubby plants with green leaves and herbs. Some are lacking in chlorophyll and thus cannot make their own food.

Monotropa uniflora L. (Indian Pipe or Corpse Plant)

The white color of the delicate, ghostly Indian Pipe, stands out against the dark, rich earth of the deep woods in which it grows. The waxy-white blossoms are borne singly on white stems from June to August. It has colorless leaf scales clasping the stem. There are two to four sepals, and six white, pinkish, or rarely red petals. The flowers are nodding until fertilized, then become erect. The clustered stems arise from a mass of fibrous rootlets. It is found in shaded woods over most of the United States. It is a saprophyte gaining nourishment from the rich humus with the aid of fungi or may become partially parasitic on the roots of other plants. The tip of the root is quite bare as the fungus is entirely post apical.(63) It often has many dark spots on it, and children who are attracted to pick it will find their prize turning completely black.

Monotropa hypopitys L. (Pinesap)

This is a closely related plant which is a yellowish-brown or pinkish color. It has scaly stems and a nodding one-sided cluster of red or yellow flowers, each of five petals and sepals. It is found blooming from June to October in the rich woods from New York to North Carolina. Romell has studied the Monotropae (77). The mycotrophic roots are entangled with hyphae and with tree mycorrhizas. Francke found that the fungus associated with M. hypopitys is a "sugar fungus" smelling like a Boletus and failing

to grow on litter or on wood. He had occasional success in raising a Monotropa away from trees. Romell believes that this does not agree with the manner in which they occur in nature, as they constantly follow their apparent host plants and occur even where there is little humus, as in dune sand. He presents the hypothesis that the monotropes are energetically epiparasites on woody plants associated with the same fungus.

Pterospora andromedea Nutt. (Pine Drops)

This plant is stout and brownish purple with a terminal cluster of nodding white urn-shaped flowers, and scale-like leaves. It grows in hard clay soil in pine woods and may be parasitic on the roots of the pine. Porter (73) says that it is now thought to be saprophytic. It has well-marked mycorrhiza and the root branching is exogeneous. This may be a special adaptation existing as a useful variation. By this method, no wound is formed.(63) It is rather rare from Canada to Pennsylvania to Michigan from June to October.

Monotropsis odorata Schwein(Sweet Pinesap) (Carolina Beechdrops)

Pinesap is a low and smooth purplish-brown saprophyte with clusters of violet-scented flowers which are white, pink, or purple in color. The corolla is persistent and rather fleshy. It is common on the Pacific coast, but rare east of the Rockies. It is found in the woods from Maryland to North Carolina blooming from April to May.

Sarcodes sanguina Torr. (Snow Plant)

Because of its early flowering habit, the bright crimson Snow Plant is often covered by a late spring snowfall. The stout, fleshy stem is almost entirely covered by masses of colorful pipe-shaped flowers with five-lobed corollas, seated among projecting conspicuous bracts. Oliver (63)

attributes the crimson color to the presence in the superficial cells of a soluble, red coloring-matter, allied probably to the tannin series. It is entirely destitute of chlorophyll.

It is reproduced vegetatively by buds from the roots, new flowering shoots arising each spring. Besides, this, the number of seeds formed is great. The roots are much branched and are associated with an investing fungal mycelium. The tissues are not as well differentiated as normal. The vascular bundles are accompanied by large quantities of parenchyma; the sieve tubes are small and not very numerous; the vessels and tracheids of the wood are narrow and often imperfectly lignified. Stomata are entirely wanting and intercellular spaces infrequent. The whole of the succulent pith and cortex of the stem consists of very thin-walled parenchyma cells, crowded with starch-granules during early stages of development; it serves as a store of food material to be used in the production of flowers and the ripening of seed. (63)

The roots are coralline in appearance of a deep-brown color and have a rough texture due to the close-fitting sheath of fungal mycelium. The fungus tubules penetrate between the epidermal cells. All lateral roots have an exogenous origin as in Pterospora. No connection exists between its roots and the pine roots among which Sarodes grows. The roots have an intimate relation with roots of other plants but are not organically united. (63) It has a capsule of a peculiar type opening by a circular cleft about the base of the style. (13)

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It is found in rich humus of high altitude forests of southern and central California, and are often found beneath Sequoias and other conifers of the Sierra Nevada Mountains. They are so striking that they were becoming increasingly rarer, until protected by regulations, and even now they occur as only scattered individuals and small colonies.

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Gentiannaceae

Several groups of this family have developed a saprophytic habit. These are found chiefly in America, but also in Asia and Africa. The plants are small, slender, low-growing herbs, containing little or no chlorophyll, and leaves reduced to scales. (75-p463)

Voyria has three species in Guiana. These have brilliantly colored scale leaves. Leiphamos, a related genus, has twenty species found chiefly in the tropical rain forests of America and the West Indies, and two in tropical Africa. The stamens in many species of both genera unite laterally forming a tube. Cotylanthera is Asiatic, while Bartonia and Obolaria are Atlantic North American, and contain some chlorophyll. (75-p463)

Convolvulaceae

Cuscuta (Tourn.) (Dodder or Love Vine)

Dodder has gone one step further than its relatives, the bindweed and Morning-glory, and depends on other plants, not only for mechanical support but also for its food and water supply. Because it is often parasitic on crop plants, such as clover and alfalfa, it has made itself a serious pest over the world. Its common names are often quite descriptive, and some may have arisen out of a farmer's ire at this pest, such as Devil's-guts, goldthread, Angel's-hair, pull-down, devil's-ringlet, hellbind, and hairweed.

Dodder is really a rather attractive plant. The brightly colored stems twine gracefully, covered with the clusters of tiny waxy white blossoms. The tough, curling stems are usually yellowish or orange but may also be white or tinged with red, and are covered by minute scales. The white, pink, or yellowish flowers appear from early June until frost. The seeds are born in fours, in capsules, which are green at first and later brownish.

Dodder reproduces vegetatively by twining from one plant to another, but also produces seeds in abundance, a single plant being capable of maturing upward of three thousand seeds. The seeds ripen from July until frost. (32)

The dodder seed contains stored-up food which it uses in germinating. The seed germinates in the ground, sending forth a slender yellowish-green shoot. This leafless, almost rootless stem rotates until it comes in contact with a suitable host. Some species may twine about almost any nearby plant, but will leave this temporary host as soon as it can climb within reaching distance of a better-liked host. If it does not find any host, it lies dormant on the soil for four or five weeks and then dies.

On reaching a suitable host, it winds itself about it from left to right and sends out innumerable tiny suckers that it sinks into the food-conducting tissues of the host and secures a supply of elaborated food. The stem then becomes somewhat yellowish or brownish but the areas where haustoria are functional are still green.(86) Hansen (32) states that the haustoria secrete diastase to dissolve the starchy substances in the host. The dodder then loses connection with the soil, and the original stem from the ground wastes away.

The dodder grows, gaining strength from its host, and reaches out to attack any other adjacent plants. Thus even though the plant first attacked may be killed by the drain upon its food supply, the dodder remains robust by the support of its new hosts. The seeds ripen early, so that they drop to the ground and may germinate to cause more infections. Half-ripe dodder seeds germinate as readily as those fully matured. (41)

Varrelman(86) points out that dodder is incorrectly spoken of as entirely devoid of chlorophyll. The germinating filament, haustoria, buds, and fruit are often quite green. In as much as plants with little chlorophyll produce more carbohydrate per unit than those with much chlorophyll, it is quite likely that Cuscuta may be able to sustain itself somewhat on its own inorganic foods. Lilienstern (51) found that dodder is able to develop chlorophyll when insufficiently nourished by the host.

Peirce (67) describes the structure of the haustoria. By the growth of the haustoria the cells of the cortical parenchyma which immediately overlie it become compressed, pushing forward, form a slight elevation on the surface of the stem. The epidermal cells composing the cushion, being now

applied to the epidermal cells of the host, exude through their own walls a solvent which attacks and dissolves the walls and contents, first of the epidermal, then of the immediately underlying cortical cells of the host. The xylem-elements of the haustoria apply themselves directly to the xylem-elements of a fibro-vascular bundle in the host.

The haustoria have an epidermis, a cortex, and central cylinder. The single layer of epidermal cells of the sucker become papillate and perform the same function as root hairs. The haustoria generally occur in groups; these do not consist of more haustoria than there are bundles in the host; thus insuring an abundant supply of food.

Cuscuta is parasitic on various herbs and shrubs. Some species are indifferent as to hosts and will attack a wide variety of species, but others have become very selective and will attack only a single genus, species, or even variety.

There are about fifty-four species of dodder in North America, Central America, and the West Indies. There are more species in the rest of the world. Lilienstern (52) made quantitative determinations of soluble carbohydrate content, finding that dodder requires a certain amount of soluble carbohydrates for its development. Lupinus luteus and Soja have a low soluble carbohydrate content and are resistant to Cuscuta. L. albus, L. angustifolia, and L. mutabilis have a higher soluble carbohydrate content and are destroyed by Cuscuta. Vicia sativa cultivated on soil with Thomas slag had a higher soluble carbohydrate content than on superphosphate and was quite destroyed by Cuscuta, while on superphosphate it was more resistant.

Lilienstern (51) made determinations of the pH of the cell saps of dodder and of various host plants. The pH of dodder was 6.2 to 6.4. Seedlings show an acidity somewhat higher than adults, the pH varying from 5.8 to 6.0. A dodder of pH 6.4 grew on Populus nigra, a common host, which averaged 6.4. Similar results were obtained with other plants on which dodder thrives. Species whose tissues have cell saps of pH 6.0 to 2.6 were not attacked.

Dean (15) listed eighty-three species of host plants for Cuscuta Gronovii Willd, the common dodder. The included 59 herbaceous, 3 twiners, 3 woody vines, 6 shrubs, 6 trees, 2 sedges, and 4 grasses. All reported hosts have been angiosperms except for the report of Yuncker that it grew on Equisetum.

Dean (16) has described the host responses to haustorial invasion of Cuscuta species. The invasion often leads to marked hypertrophy of adjacent tissue, resulting in gall formation. At the point of initial attack typically a short bulbous hypertrophy is developed. Similar swellings are formed at points of secondary infection. Living dodder tissues buried within a gall may regenerate new stems reproducing the plant vegetatively.

Dodder causes much damage to cultivated crops. It is particularly troublesome in southern California, Virginia, Utah, Kentucky, and Colorado, and in all regions where clover and alfalfa are raised for seed. It is a terrible pest in Europe where, in some regions, the production of clover seed has stopped because of the ravages of dodder.

Many species of dodder grow on wild plants. There are six species disseminated with commercial seed, thus becoming pests chiefly on farm plants. (41) C. epilinum Weihe (Flax dodder) is prevalent in foreign fields

and has been introduced in America with seed. This is the only species parasitic on flax here.

C. epithymum Murr. (C. trifolii) (Clover dodder) infests both true clovers and alfalfa. It is found in Europe, and in America, east of the Mississippi river and in the North Pacific states.

C. planiflora (Small-seeded Alfalfa dodder) appears to confine its attack to alfalfa in preference to true clovers. This is by far the most abundant and destructive of the dodders in the western states.

C. arvensis Beyrich (Field dodder) is widely distributed throughout the United States. It infests both clovers and alfalfa and also many wild herbaceous plants.

C. indecora Chois (Large-seeded alfalfa dodder) is common in the west, especially in Utah. It attacks a number of plants but prefers leguminous crops, particularly alfalfa.

C. racemosa chileanna (Chilean dodder) attacks clover and alfalfa. It is not common here but is of interest as its seeds are frequently found in red-clover and alfalfa seed imported from South America.

The kinds of commercial seed infested with dodder are mainly flax and leguminous crops, and confined to those whose period of ripening coincides with that of the dodder, and whose seeds are small enough to admit the dodder seeds as an impurity. The farmer raising host crops of dodder should acquaint himself with the sizes and characteristics of the seeds. Dodder may be partially removed from impure seeds by screening. Meshes of a certain size for the different species are used as a sieve.

When dodder appears on a farm, steps should be taken to eradicate it immediately so that it will not gain a strong foothold. Small patches

may be destroyed by cutting before the seed matures or sprinkling with crude oil or kerosene, and burning when well dried, or burned with a blow torch. Afterwards the infested area should be cultivated frequently for three weeks to induce any surviving seeds to germinate and destroy seedlings.

When a whole crop is dodder-infested, it should be cut before the flowers open as dodder frequently matures seed after the crop upon which it is growing has been cut. If the dodder has gone to seed, the crop should be mowed and burned to kill the plants and the seeds on the soil surface. Various chemical sprays are used but are expensive, difficult to apply, usually kill the host too, and are not completely successful. Pasinetti(65) found 3-10 per cent monochloracetic acid was sufficient to prevent the growth of Cuscuta. In infested crops, such as lespedeza, dodder may be controlled by grazing heavily. Dodder does not poison stock and cattle will eat it readily. (71)

The seeds may remain in the ground and germinate after several years, so that other crops not susceptible to dodder should be rotated in a five-year cropping plan with the host crops.

Scrophulariaceae

The Figwort family contains many herbs, a few of which are root parasites.

In the genus Gerardia, the species vary from leafy, independent plants, to G. purpurea, to G. olizophylla with few pale green leaves, to the most degraded species, G. aphylla, in which the leaves are only small, pale green scales and have few stomata. The roots also vary from none, to a few or many suckers, parasitic on grasses, composites, etc. The root has much more xylem than phloem. The roots produce swellings in the region of contact with the host, which become hemispherical and grow down the sides of the host roots but do not completely surround them. Sections of swellings show an epidermis, a cortex, and bundle elements. In the lower part of the swelling, vessels appear more marked and established connections with the xylem of the host roots.

The genus Castilleja (Painted Cup) also contains herbs which are root-parasitic. The flowers are yellow or reddish in spikes. They have green leaves.

Orthocarpus is a genus of parasitic annuals. O. purpurascens appears in the spring on the deserts of the west if there has been sufficient rain. It is parasitic on eighteen species, all but two of which are annuals. (54)

In Melampyrum pratense (Cow Wheat) haustoria appear on young roots of seedlings and their formation is not dependent on the presence of the host. They arise laterally and never terminate the roots. (54)

Some members of the genus Euphrasia (Eyebright) are also root-parasitic. The leaves and stem are purplish-red. The roots have little whitish

swellings attached to the roots of other plants, generally grasses. The hosts include Poa, Avena, Festuca, Carex, Luzula, Capsella, Trifolium, Epilobium, and Senecio. Selageanu (78) found that the assimilation of carbon dioxide was greater in Trifolium than in Euphrasia.

Lathraea (Toothwort) is more a decided root parasite on hazel, beach, and other trees. Its vegetative axis has become a rhizome two to six inches long, and it is provided with hollow-scale leaves. From the annual, short-lived inflorescence, numerous flowers arise. It is destitute of chlorphyll. The subterranean stems have a fleshy, solid, elastic appearance and are covered with thick, squamous leaves. The leaves are broadly cordate. (3) The scales are underground and have lost their vegetative function, but they are rolled back in such a way as to form peculiar, irregular cavities which open to the outside near the tip of the leaf. These catch animal prey which die there, and their remains supplant the diet of the plant. (22) Its common name is Toothwort because of the resemblance of the scales to teeth. In mediaeval times, it was thought to be a remedy for toothache. Heinricher (40) believes that Lathraea seeds must be in contact with roots of the proper host in order to germinate. Chemin(9) found, however, that they would germinate on sand, or moist cotton in either light or darkness. The food reserve in the cotyledons permits development of a young seedling, but since the seed lacks chlorophyll, it must become associated with the host, for continued existence. Hartley and Holmes (38) believe that Lathraea is able to exist as a saprophyte also because active haustoria were found penetrating dead and decaying roots in two widely separated stations.

Orobanchaceae

Boeshore (3) points out that the Orobanchaceae are in direct morphological continuity with the Scrophulariaceae. This family is well-known for its parasitic habits and many of its species harm cultivated plants.

Epifagus virgiana (L.) Bart. (Leptamnium or Epiphegus)
(Beech Drops or Cancer Root)

Beechdrops are slender, growing from six inches to two feet high. The plant is purplish or yellowish-brown, much branched. Its leaves are reduced to small scattered scales. It has a tuberous swelling which represents a fused primary root below and a greatly condensed vegetative stem-axis above. From the lower part, or primary root, short, functionless rootlets start. From the condensed stem, adventitious roots arise at any point of the stem axis. Parasitic connection with the host is easily and directly made by the germinating primary root. The roots of Epifagus form around and above the beech roots on which this is parasitic. The secondary and adventitious roots are short and delicate. The host roots seldom remain alive beyond the point of attachment. (2) The white corollas are tinged with pink or purple above. The corolla and calyx teeth have narrow lines of brown madder. Weatherby (89) describes f. pallida in which these striae of madder pigment are lacking which is found in old beech and maple woods in Vermont. Epifagus blooms from August to October. Its range is from Nova Scotia to Florida and from Ontario to Louisiana.

Conopholis americana (L.f.) Wallr. (Squaw-root)

Percival (68) has made a thorough study of this parasite. The mature plant consists of one or more fleshy flowering spikes and a portion of the tubercle from which the spikes have arisen.

The tubercle is always terminal on the parasitized root although, eventually appearing lateral owing to the further elongation of a root secondary to the first. The flowering shoots vary from light tan to chestnut brown, and are entirely devoid of chlorophyll. Nodules are very irregular and tend to be round with the constantly enlarging circumference overlapping somewhat the host root. From half to most of the flowering shoot is fertile with out 50 very closely massed flowers, which are spirally arranged. Each flower is in the axil of a scale-like bract. Below the inflorescence, the shoot is covered by many scales.

The line of juncture between the tissues of the host and those of the parasite is very sharp though quite uneven. The xylem and phloem of the parasite were traced through the nodule to the xylem and phloem of the host. The phloem of the parasite is apparently non-functional. Host reactions consist of changes in the pitting and form the trachery tissues, and in the tannin infiltration of the parenchyma cells adjacent to the parasite tissue.

Many attempts at germination with and without hosts under varied conditions failed. In one experiment, the radicle of a germinating seed penetrated an actively growing red oak root tip. C. americana parasitizes Quercus borealis from southern Maine to Michigan, south to Florida and Tennessee. It is comparatively rare. It has been collected in Massachusetts from Fall River and Freetown, and from Tiverton, Rhode Island. (78)

Orobanche (Aphyllon or Thalesia) (Broom Rape) is a group of dully colored parasites lacking in chlorophyll. They are parasitic on grains, herbs and shrubs, and many are great pests in southern Europe. Species introduced from Europe are common in eastern fields, and there are many native species west of the Rockies. Most of them have slender, whitish, yellowish, or

purple-colored shoots with a few scale-like leaves and a terminal spike of urn-shaped flowers. The curved corolla has an erect and two-lobed upper lip and a spreading three-lobed lower one. (42)

The vegetative axis is one and one half inches or less in length. It is a shortened but enlarged tuber, covered densely with crowded scales. (3) Orobanche is often called Broom rape because it is parasitic on broom, a legume.

Orobanche uniflora L. (One-flowered Cancer-root). Several tan, much branched shoots arise from the subterranean stem bearing scales and flowers. It is not greatly restricted as to hosts parasitizing plants like goldenrod, aster, and sedum.

O. ramosa L. (Branched Broom-rape) is common on hemp and tobacco in Kentucky and Illinois and has been reported on tomato and a green-house Coleus. (61) It bears racemes of bluish-yellow flowers on much branched stems in July. It parasitizes many plants; twenty-nine hosts are given.

O. fasciculata (Cancer-root) has dull yellow stems with yellowish-tan blossoms. It is parasitic on Eriogonum, Cannabis, and Artemisia.

O. minor is parasitic on clover and about forty other plants.

Conclusions

1. There are three distinct types of dependent forms; parasites on the roots of the host, parasites on the aerial parts of the host, and saprophytes.
2. Plants lacking in chlorophyll cannot manufacture sufficient starch for their needs and must rely on the host for some or all elaborated food. Loss of chlorophyll is not a necessity but is often an accompaniment of parasitism.
3. The degree of parasitism may vary greatly; Viscum album contains chlorophyll and carries on photosynthesis; Cuscuta seedlings are autophytic but soon become holoparasites; Rafflesia is entirely within the host, except for the huge blossom nourished by the food which it usurps.
4. In determining the type and degree of dependency, the plants are studied to find the number and structure of parasitic attachments. The greater number of haustoria, the greater is the reliance on the host. If the haustoria connect with sieve tubes, the parasite can take nutrients from the host. Those lacking these connections may tap the water and minerals in solution in the xylem from which they make their own food.
5. Parasitic attachments follow the line of least resistance (seen expecially in artificial parasitism and in mistletoe,) and cannot penetrate material which has toughened.
6. The location at which the parasite is attached to the host is often marked by deformities.

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6. The location at which the parasite is attached to the host is often marked by deformities.

7. Parasites often reproduce vegatatively by the endophytic system or aerial parts. They also produce many seeds which frequently have efficient methods of dissemination.
8. The parasitic plants may have originated from primitive autophytic plants. Parasitic plants occur in widely separated families, indicating many separate points of origin.

Abstract

The "slackers" among the seed plants include a great number of varied forms and types. These dependent plants are heterotrophic in contract to autophytic plants, which obtain all their water and food materials directly from the soil or air and contain chlorophyll to manufacture dextrose in sunlight. The degree to which the parasite is dependent on the host may vary. There are certain characteristics more or less common to all dependent seed plants. There is some means of connection with the host, such as haustoria. There may be a loss of chlorophyll. Vegetative parts may be reduced in size. The parasite frequently produces an abnormal effect on the host.

Parasitism of one seed plant on another has been induced successfully in experiments when the same general conditions as those found in nature are observed. Many plants are easily made to become artificial parasites showing that the tendency toward artificial forms is strong.

Many saprophytes are found among the Orchidaceae. These often have a coral-like mass underground, covered by a fungal mycelium which enables them to secure their food. Several species of New England orchids are saprophytes. Some tropical members of this family are parasites.

The Loranthaceae is the parasitic family of mistletoes. Viscum album is the mistletoe of Europe, and Phoradendron flavescens that of America. These are a golden-green color and contain chlorophyll. They require only water and the substances dissolved in it from their host trees. Arceuthobium is the minute genus parasitic on conifers and causing much damage in the forests of the Western United States. There are many tropical mistletoes, some of them attacking rubber trees, and others harming cultivated plants.

The seeds of mistletoe are sticky to make them adhere to the branches of the host, and to aid in their dissemination by birds and other animals.

Seed plants parasitic on the roots of their hosts are found among the following families; Santalaceae, Rafflesiaceae, Hydnoraceae, Balanophoraceae, Ericaceae, Scrophulariaceae, and Orobanchaceae. Some root parasites seem to be able to live autophytically, while others such as Rafflesia have reached a high degree of dependency.

There are two genera of parasites, Cuscuta and Cassytha, which wind around their hosts, sinking haustoria into its stem.

Parasites have been found to have in general a higher osmotic pressure than their hosts. It would be interesting to compare other factors of hosts and parasites to see if they are constant among the dependent families. The metabolic rates of natural and artificial parasites could be investigated.

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Explanation of Plates

Plate I

Fig. 1 Opuntia on Sahuaro
2 Sahuara with Opuntia in cavities of summit
3 Section showing the development of roots of cissus in opuntia
4 Cissus digitata parasitic on Opuntia blakeana (from 54)

Plate II

Fig. 1 Corallorrhiza trifida
2 C. odontorhiza
3 C. Wisteriana
4 C. striata
5 C. maculata
(Adapted from Morris and Eames 53)

Plate III

Fig. 1. Surface view of the stomata of oak (o) and mistletoe (m) to show relative size
2. Cross section of an oak branch showing sinkers (s)
3. Oak branch and Mistletoe attached (from 55)

Plate IV

Fig. 1 Cross section of a larch trunk with a large burl
2 A common type of original infection on a larch branch showing the beginning of witches' brooms (Weir 87a)
3 Phoradendron crassifolia on Hevea (from photograph 89)
4 Phthirusa brasiliensis on Hevea (from photograph 89)
5 Pseudotsuga taxifolia infected with A. douglasii (88)

Plate V

Fig. 1 Brooms in black spruce caused by Arceuthobium pusillum
2 Fruit of A. pusillum
3 & 4 Distribution of A. pusillum and Picea (Eaton and Dow 19)

Plate VI

Fig. 1 A. pusillum (Eaton and Dow 19)

Plate VII

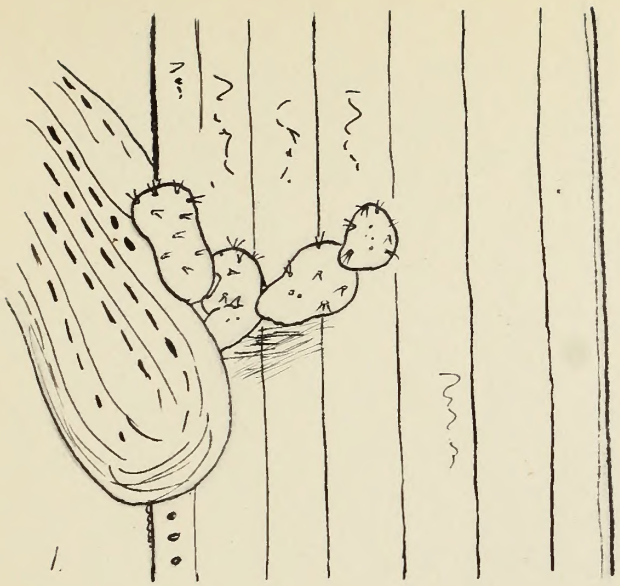
Fig. 1 Monotropa uniflora
2 Orobanche uniflora
3 Epifagus virginiana
4 Corallorrhiza maculata

Plate VIII Seeds of Alfalfa and Dodder enlarged and natural size

Fig. 1 Alfalfa
2 Small-seeded Dodder (C. epithymum)
3 Large-seeded Dodder (C. trifolii)
4 Young alfalfa plants attacked by Dodder (fron 34)
5 Dodder in flower
6 Galls caused by Dodder (15)

Plate IX

Fig. 1 A nodule bearing flowering shoots of Conopholis americana on a root of Quercus borealis. The shoots are in fruit.
2 Young C. americana nodules showing the development of secondary roots (68)
3 Root system of Gerardia flava showing parasitic attachment
4 Stem and root system of Aphyllon uniflorum parasitic on roots of Aster corymbosum.
5 Orobanche
6 Epifagus
7 Conopholis



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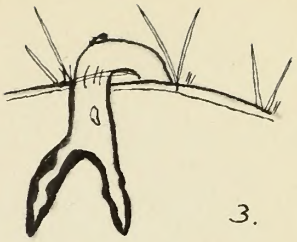

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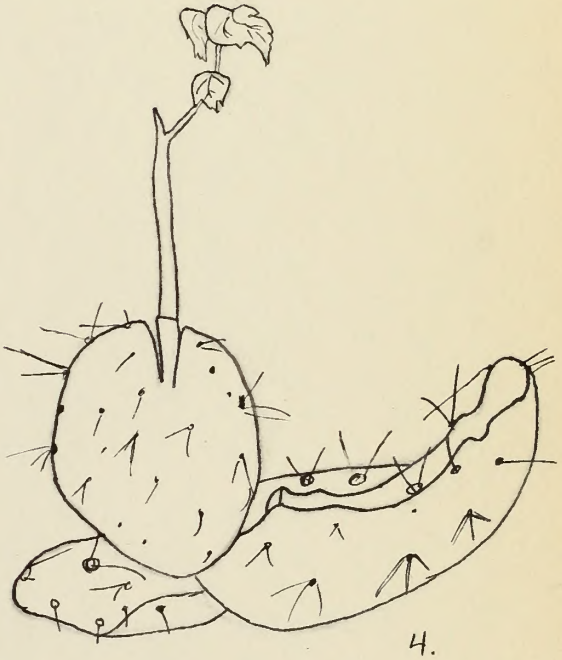

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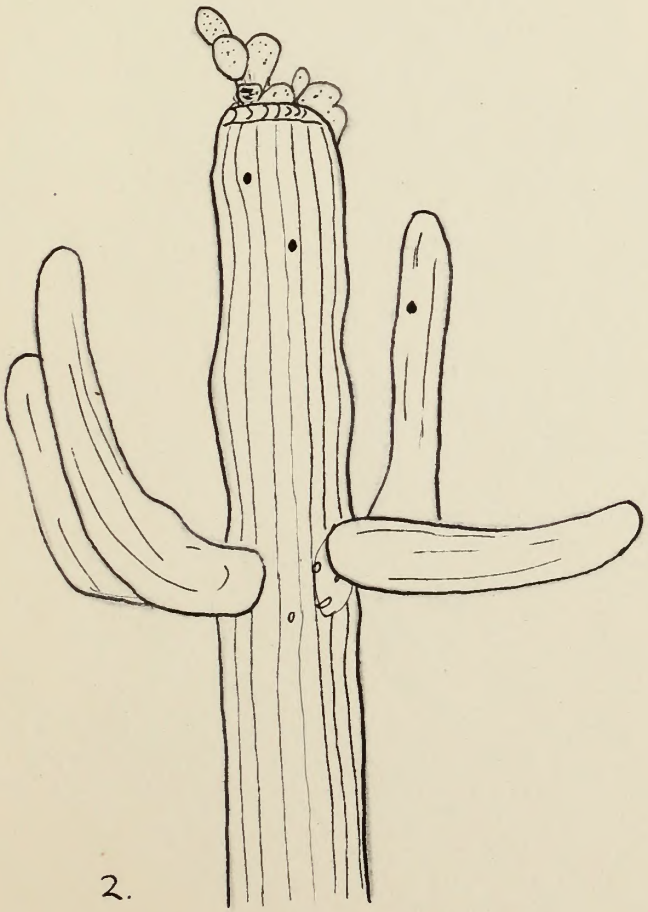

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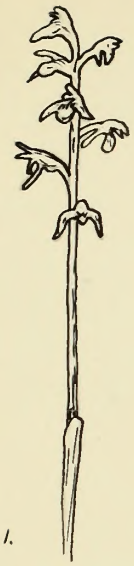

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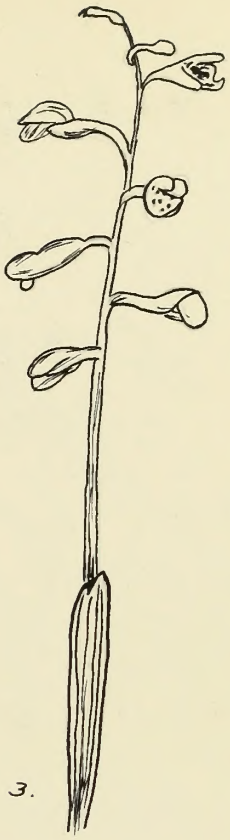

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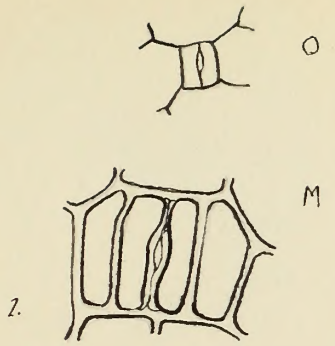
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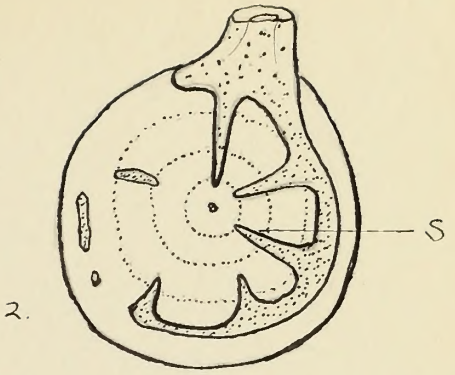
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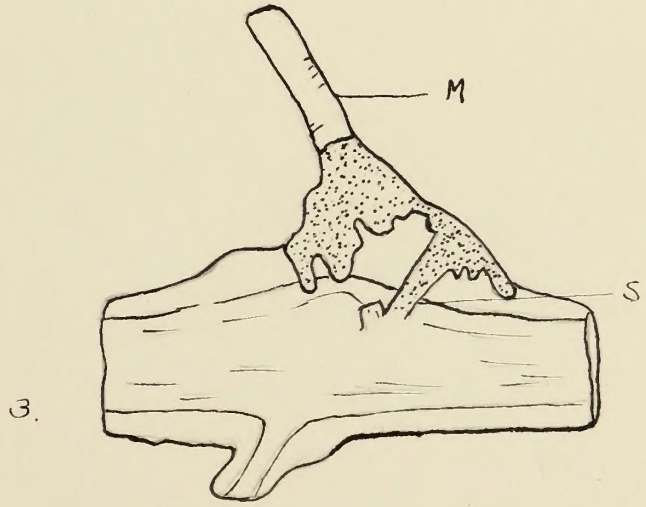
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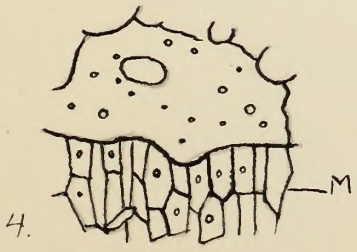
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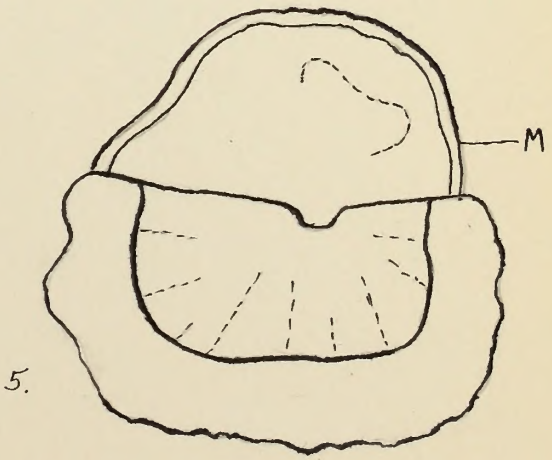
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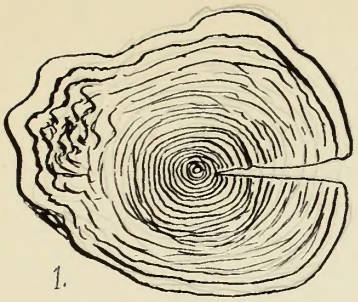

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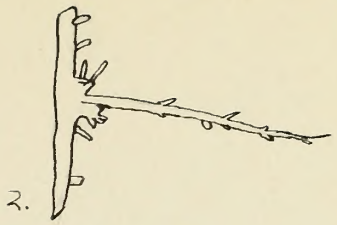

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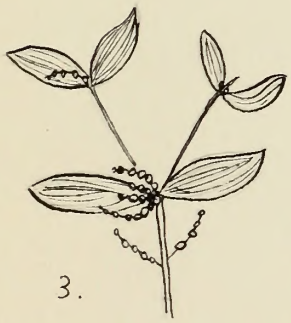

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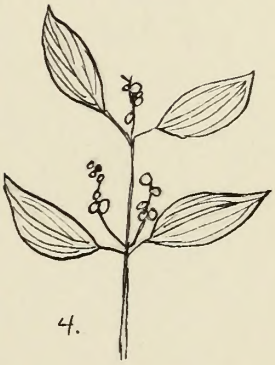

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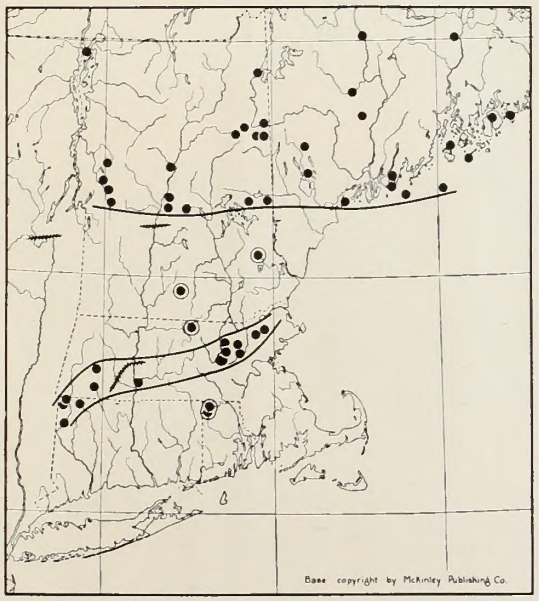

The distribution of the dwarf mistletoe in New England. Notice the five isolated stations (in circles) which lie outside both the northern area and the narrow band to the south. The jagged lines show the positions of moraines deposited during the retreat of the continental ice.

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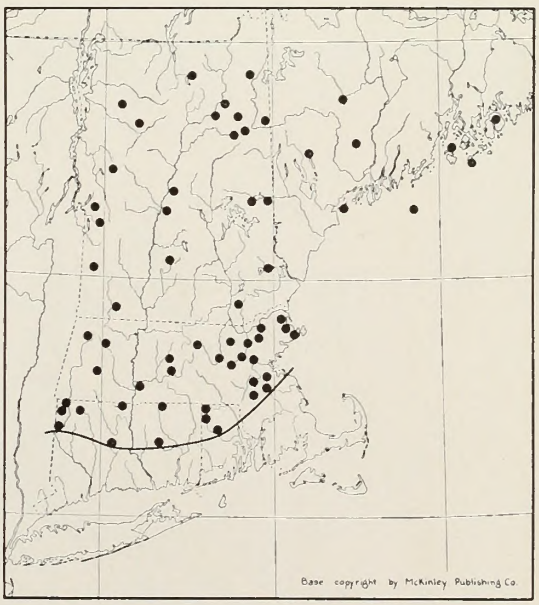
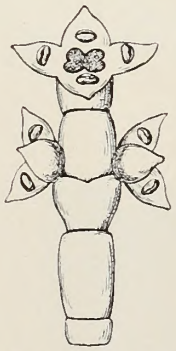


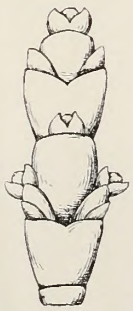
The distribution of black spruce in New England. Each spot marks a locality represented by specimens in one or more herbariums. The heavy line indicates the southerly limit of the tree.

4.

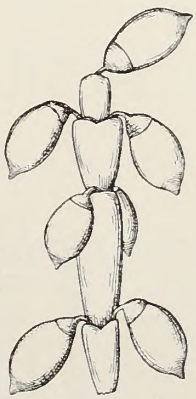
The large male plant (left), with four or more flowers, and the female plants (right), also in blossom, are shown more than twice natural size. The male plant was only five-eighths of an inch high!



Male plant in flower (about 3x).



Female plant in flower (about 3x).



Plant with ripe fruit (about 4x).

Sketches by Mr. C. E. Faxon. Courtesy of Rhodora.

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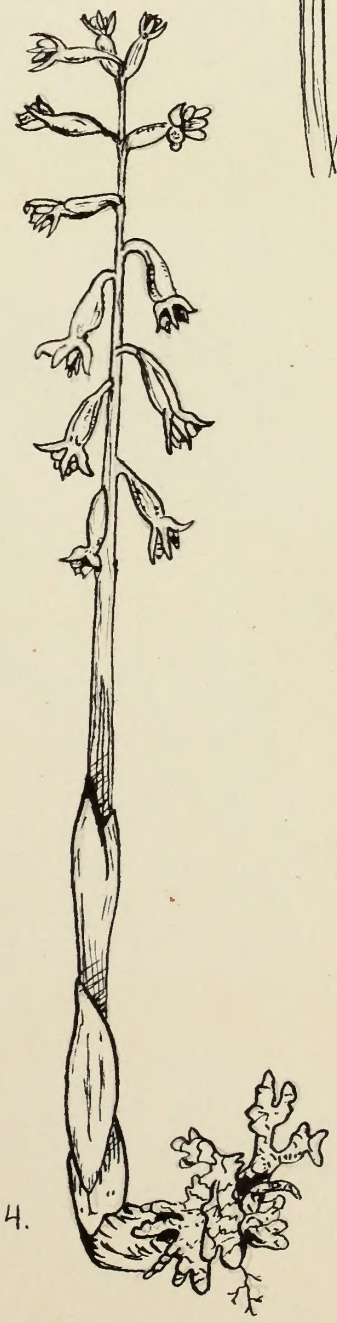

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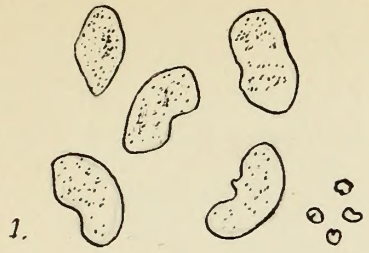
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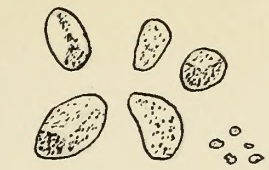
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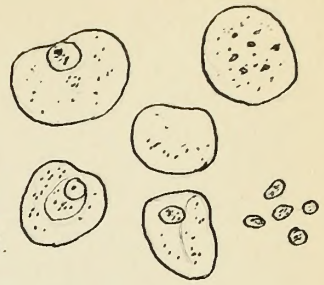
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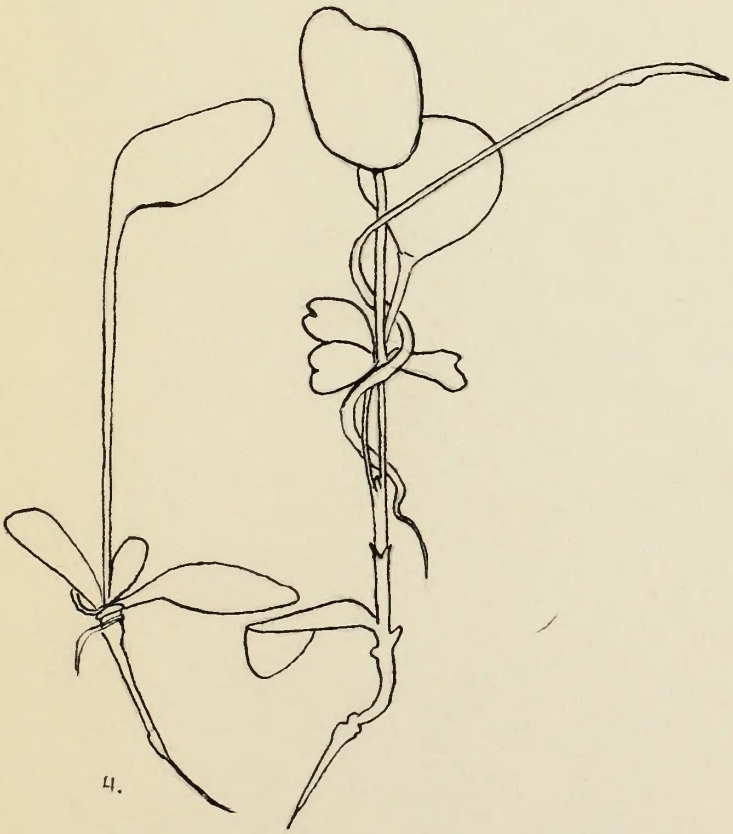
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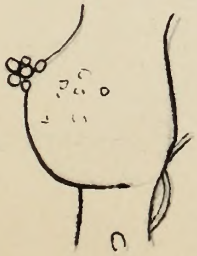


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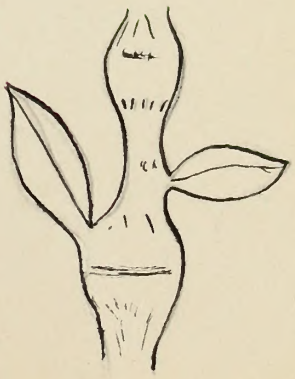

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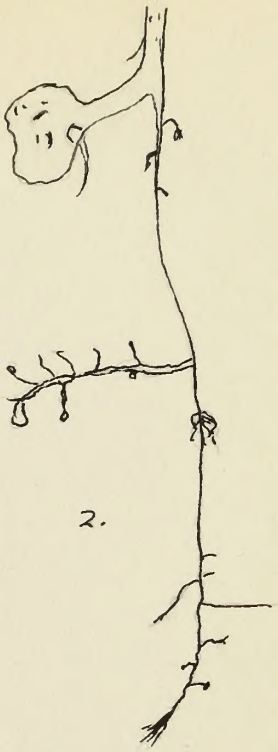

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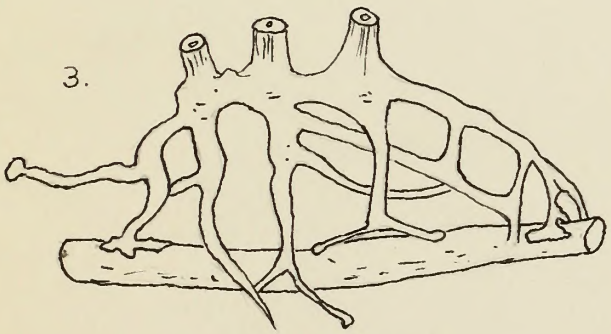

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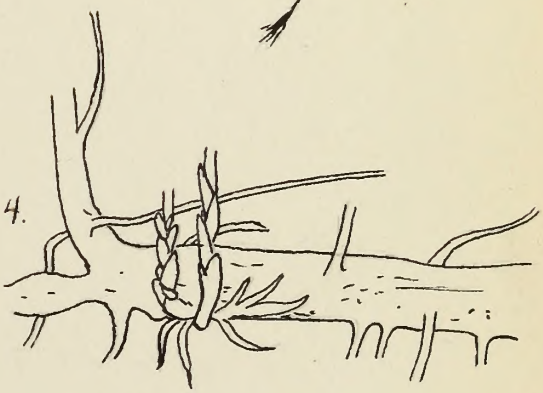

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